The cascade of uncertainty in modeling forest ecosystem responses to environmental change and the challenge of sustainable resource management

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Abstract

Increasing human activities have triggered environmental changes. These threaten the life-supporting systems that thus far have enabled continuous improvement of humanity's living conditions. Projecting the effects of environmental change on social-ecological systems is a crucial component of sustainability science and a cornerstone for the sustainable management of natural resources. Such projections rely on models and modeling chains. In climate change impact assessments, such a modeling chain reaches from socioeconomic scenario modeling through General Circulation Models to impact and management/policy models in specific sectors. At each modeling step, model-specific uncertainties about parameter values, input data or structure accumulate and lead to a cascade of uncertainty. In past impact assessments such as those presented in the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, these uncertainties have only been partly considered. This has cast doubt on the robustness of scientific findings. Therefore, it is crucial that current uncertainties about management-relevant scientific findings are appropriately assessed since decision-makers need to base their decisions on the best-available knowledge.

The aim of this thesis is to explore the cascade of uncertainties in responses to environmental change in a structured way at the example of forest ecosystem modeling. This leads to two overarching research questions:

1. How do different types of uncertainties affect projections of the effects of environmental change on forest ecosystems?
2. What is the general framework of sustainable natural resource management in coupled social-ecological systems in which uncertainties need to be integrated?

I addressed these questions by combining quantitative and qualitative research. Firstly, I applied the process-based forest growth model 4C to forest stands across Europe (chapters 3-5). Secondly, I synthesized a large body of scientific literature to develop novel frameworks for characterizing specific types of uncertainties (chapters 2 and 6) and for describing the wider framework in which uncertainties have to be included to enhance the sustainable management of natural resources (chapter 7).

This thesis shows that forest productivity under climate change may increase in cool and wet regions and decrease in already warm and dry regions. These findings are robust despite large differences in model structure (chapter 2), climate change scenarios (chapter 3) and model parameters (chapter 4) that induce considerable uncertainty into future projections. It also stresses that there are methods available to assess uncertainties (chapter 5) but also that many climate change impact studies in forests have focused on testing the response of plants to changes in mean climate rather than climatic extremes (chapter 6). The latter may however ultimately shape the responses to climate change in reality. Finally, this thesis shows that adaptive, cross-sectoral natural resource management strategies exist that accommodate uncertain impacts of environmental and societal change and foster sustainable regional development (chapter 7).

I conclude that the cascade of uncertainty challenges sustainable natural resource management and that a more systematic treatment of uncertainties is strongly needed to generate robust projections of the impacts of environmental change on natural resources. The findings of this thesis provide a general framework in which both modelers and decision-makers can integrate model results and assess their robustness. This work ultimately contributes to science-based adaptive management and learning that are an integral part of the transformation toward resilient and sustainable social-ecological systems.

Keywords: Adaptation, Climate change, Environmental change, Forest ecosystems, Impact studies, Global Change, Models, Uncertainty, Sustainable resource management, Vulnerability

Zusammenfassung

Die durch den Menschen verursachten Umweltveränderungen bedrohen genau die lebenserhaltenden Systeme, die bisher eine stetige Verbesserung der Lebensqualität der Menschheit ermöglicht haben. Projektionen der Effekte dieser Umweltveränderungen auf sozio-ökologische Systeme sind ein fester Bestandteil der Nachhaltigkeitsforschung und ein Kernelement des nachhaltigen Managements natürlicher Ressourcen. Solche Projektionen beruhen auf Modellen und Modellketten. In Klimawandelwirkungsstudien reicht eine solche Modellkette von sozio-ökonomischen Szenarien über globale Zirkulationsmodelle hin zu Wirkungs- und Management- bzw. Politikmodellen in bestimmten Sektoren. In jedem Modellierungsschritt werden modelspezifische Unsicherheiten bezüglich Parameterwerten, Eingabedaten und Modelstruktur akkumuliert und führen zu einer Kaskade der Unsicherheiten. In früheren Wirkungsstudien, wie zuletzt dem 4. Sachstandsbericht des „Intergovernmental Panel on Climate Change“, wurden diese Unsicherheiten nur teilweise berücksichtigt. Das hat Zweifel an der Robustheit wissenschaftlicher Erkenntnisse aufkommen lassen. Daher ist es notwendig, dass Unsicherheiten über managementrelevante wissenschaftliche Ergebnisse angemessen eingeschätzt werden, um Entscheidungsträgern die bestmögliche Entscheidungsgrundlage zu bieten.

Ziel dieser Dissertation ist es, die Kaskade der Unsicherheiten der Wirkungen von Umweltveränderungen am Beispiel der Waldökosystemmodellierung auf strukturierte Art und Weise zu behandeln. Dies führt zu zwei übergreifenden Forschungsfragen:

1. Wie beeinflussen unterschiedliche Typen von Unsicherheiten die Projektionen der Wirkungen sich verändernder Umweltbedingungen auf Waldökosysteme?
2. Gibt es einen übergeordneten Rahmen für nachhaltiges Ressourcenmanagement in sozio-ökologischen Systemen, in den Unsicherheiten eingebettet werden können?

Diese Fragen habe ich mittels quantitativer und qualitativer Methoden untersucht. Erstens habe ich das prozess-basierte Waldwachstumsmodell 4C in Waldbeständen in ganz Europa angewendet (Kapitel 3-5). Zweitens habe ich eine Vielzahl wissenschaftlicher Arbeiten synthetisiert, um Rahmenbedingungen zur Charakterisierung bestimmter Typen von Unsicherheiten zu entwickeln (Kapitel 2 und 6) und um das weitere Umfeld darzustellen, in dem Unsicherheiten betrachtet werden müssen, um nachhaltiges Management natürlicher Ressourcen zu verbessern (Kapitel 7).

Diese Dissertation zeigt, dass die Produktivität von Wäldern unter Bedingungen des Klimawandels in kühleren und feuchteren Regionen zunehmen und in wärmeren und trockeneren abnehmen kann. Diese Ergebnisse sind qualitativ konsistent über eine Vielzahl von Modellstrukturen (Kapitel 2), Klimaszenarien (Kapitel 3) und Modelparameter (Kapitel 4), die jedoch quantitativ zu nennenswerten Unsicherheiten in Projektionen führen. Diese Arbeit zeigt ebenfalls, dass es Methoden gibt, um bestimmte Unsicherheiten einzuschätzen (Kapitel 5). Sie verweist aber auch darauf, dass viele Klimawirkungsstudien die Wirkung von Veränderungen im Mittelwert von Klimavariablen betrachten und nicht die von Extremwerten (Kapitel 6). Außerdem veranschaulicht diese Dissertation, dass adaptive, sektorenübergreifende Strategien für ein nachhaltiges Ressourcenmanagement existieren, die mit Unsicherheiten von Klimawirkungen umgehen können und nachhaltige, regionale Entwicklungen fördern (Kapitel 7).

Ich folgere daraus, dass die Kaskade der Unsicherheiten eine zentrale Herausforderung für nachhaltiges Ressourcenmanagement ist. Eine systematischere Behandlung von Unsicherheiten ist erforderlich, um robuste Projektionen der Wirkungen sich verändernder Umweltbedingungen auf natürliche Ressourcen zu ermöglichen. Die Ergebnisse dieser Dissertation veranschaulichen ein Bezugssystem, in das Modellierer und Entscheidungsträger Modellergebnisse integrieren können um deren Aussagekraft einzuschätzen. Damit leistet diese Dissertation leistet einen Beitrag zum wissenschaftsbasierten, adaptiven Management, das ein zentraler Teil der Transformation zu resilienten und nachhaltigen sozio-ökologischen Systemen ist.

Schlagwörter: Anpassung, Globaler Wandel, Klimawandel, Modelle, Nachhaltiges Ressourcenmanagement, Umweltwandel, Unsicherheiten, Vulnerabilität, Waldökosysteme, Wirkungsstudien

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1 General introduction

Increasing human activities over the past century have triggered a plethora of environmental changes (Steffen et al. 2011). The most substantial ones include climate change (IPCC 2007a), biodiversity loss (Barnosky et al. 2011; Butchart et al. 2010), alterations of the nitrogen cycle (Galloway et al. 2008; Canfield et al. 2010), deforestation (Williams 2006) and other land system changes (Turner II 1990; Foley 2005). Such pervasive alterations of the earth system threaten the very life-supporting systems that thus far have enabled continuous improvement of humanity's living conditions (Millennium Ecosystem Assessment 2005; Rockström et al. 2009). They culminate in what Clark et al. (2004) have termed the 'Anthropocene crisis'.

The awareness of the magnitude and importance of the Anthropocene crisis has framed a new interdisciplinary research field – sustainability science (Kates et al. 2001; Reid et al. 2010; Bettencourt & Kaur 2011). Sustainability science recognizes that people and nature are interacting in coupled social-ecological systems (Liu et al. 2007). In such social-ecological systems, the management of natural resource systems is a key interface of nature and society. Hence, sustainable management has emerged as the leading paradigm of natural resource management to guarantee ecosystem functions and services for current and future generations and to steer transformations towards a sustainable future.

Sustainable natural resource management requires (1) projecting the impacts of environmental change on social-ecological systems, (2) assessing the vulnerability of social-ecological systems to environmental change and (3) weighting the options to adapt to environmental change. Thus, it relies to a large extent on models and model chains, especially if future developments under climate change are studied. Model chains consist of a set of models that are connected through information flow. For example, climate change scenario data generated by a General Circulation Model (GCM) may be used to drive a species distribution model that projects the occurrence of a certain species in a specific habitat under climate change. These model chains can be very complex and reach from socioeconomic scenario modeling through GCMs and Regional Climate Models (RCMs) to impact and management/policy models in specific sectors. At each of the steps in the model chain, model-specific uncertainties about, amongst others, parameter values, input data or model structure accumulate. This leads to a 'cascade of uncertainty' (Schneider 1983; Jones 2000; Fig. 1-2).

In past vulnerability, impact and adaptation assessments such as those presented in the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2007b), the cascade of uncertainty has only been partly considered. However, today's decisions constrain future options through lock-in effects (WBGU 2011). For example, investment in specific technology limits future technology switching just as the choice of tree species to be planted in a forest determines the forest development for the next 100 years. Therefore, it is crucial that current uncertainties about management-relevant scientific findings are appropriately assessed since managers and decision-makers need to base their decisions on the best-available knowledge. Otherwise, it is unclear how robust scientific findings are, how pressing the transition to climate-resilient sustainable development pathways is but also how current environmental changes may be turned into opportunities for transformational adaptation. Hence, the cascade of uncertainties of the responses of social-ecological systems to environmental change challenges the sustainable management of natural resources.

The objective of this thesis is to explore the cascade of uncertainties in responses to environmental change in a structured way at the example of forest ecosystem modeling. Therefore, I will now briefly introduce forest ecosystems under environmental change and then present a theoretical framework of uncertainties in model chains.

1.1 Forests and environmental change

Forests are coupled social-ecological systems since they provide many important functions and services to human societies and since they are affected by anthropogenic, environmental change. The latter holds true even for remote, virtually untouched old-growth forests across the globe (Laurance et al. 2004; Luyssaert et al. 2008; Lewis et al. 2009).

Forests cover about 31% of the global land area (FAO 2010) and harbor a large part of terrestrial biodiversity (Mace et al. 2005). They are crucial components of the earth system for example through the large amounts of carbon they store (Reich 2011) or through their feedbacks with the regional climate and water balance (Bonan 2008; Anderson et al. 2011). Forests also provide a multitude of goods and services to humanity. The estimated value of forest product removal was 121.9 billion USD in 2005 (FAO 2010). This is however only marginal compared to the estimated value of other ecosystem services provided by forests such as nutrient cycling or climate regulation which do not have a market value (Costanza et al. 1997).

Forests are and will continue to be affected by climate change (Lindner et al. 2010; Heyder et al. 2011) but these climate change impacts occur in concert with and interact with other environmental changes that also affect forests. These environmental changes include an increase in atmospheric carbon dioxide concentration (Tans & Keeling 2012), nitrogen deposition (Dentener et al. 2006), ozone (Ashmore 2005), and deforestation (Williams 2006). Aber et al. (2001), Hyvönen et al. (2007) and Chmura et al. (2011) present more detailed reviews of the effects of environmental change on forest processes. With regard to climate change, forests are not only considered to be vulnerable to a changing climate (e.g. Lindner et al. 2010) and to be part of the problem due to mainly tropical deforestation (Houghton 2003; Canadell et al. 2007) but also to be part of the solution due to their importance as carbon sinks (Canadell & Raupach 2008; Reich 2011) and potential sources for bioenergy (Chum et al. 2011). However, strong concerns about trade-offs of forests managed for climate change mitigation and other functions remain (Hudiburg et al. 2011; Whitehead 2011; Schulze et al. 2012). Furthermore, there are strong concerns about how to adapt forests and forest management to a changing climate that adds on an already long list of other stresses on forests (Seppälä et al. 2009).

The impacts of climate change in particular and environmental change in general on forests are often studied using process-based forest models. Stand-scale, process-based models (PBMs) are particularly suitable for this task since they rely on a mechanistic understanding of forest processes and hence account for changing environmental conditions (Mäkelä et al. 2000; Landsberg 2003; Fontes et al. 2010). Furthermore, they allow for integration of forest management. Medlyn et al. (2011) provide a more detailed discussion of different forest model types that maybe used for climate change impact assessments.

1.2 Theoretical framework of uncertainties

In this thesis, I define uncertainty according to Walker et al. (2003) as “any departure from the unachievable ideal of complete determinism.” This implies that there will always be uncertainty. I briefly introduce different dimensions and types of uncertainties following and adjusting the classification of Walker et al. (2003) and discuss how uncertainties accumulate along a ‘cascade of uncertainty’ (Schneider 1983; Jones 2000) in assessments of climate change impacts on forest ecosystems and of the subsequent derivation of management and policy options. I focus on uncertainties from a modeling perspective because models play a crucial role in climate change impact assessment but the framework of different dimensions and types of uncertainty also accommodates other perspectives of uncertainties. The

different dimensions and types of uncertainty are universal but their importance varies in different research approaches.

1.2.1 Dimensions and types of uncertainties

Walker et al. (2003) defined three dimensions of uncertainty, namely the *location*, the *level* and the *nature* of uncertainty. Each of these dimensions contains different types of uncertainties which result in an uncertain output of a specific model application. I adjust and simplify this framework to suit uncertainties in climate change impact studies but for more complete descriptions and definitions see van Asselt & Rothman (2002) and Walker et al. (2003).

Location of uncertainty

Uncertainty is located within a model in the model *structure*, *input* and *parameters* (Walker et al. 2003). The *model structure* represents the relation of the different variables, processes and underlying assumptions that are part of the model. It relates to the processes included in the model (e.g. which photosynthesis model or which management algorithms), the level of detail of process descriptions and the formulation of mathematical equations. The definition of the system boundaries, scaling issues and whether the model results are deterministic or stochastic are also part of the model structure. GCMs for example do not yield the same results if run twice with exactly the same input, parameters, boundary conditions etc. since they contain non-linear elements (Le Treut et al. 2007). Another important part of the model structure is how the computer implementation of the model is realized. Uncertainties related to the model structure are henceforth referred to as structural uncertainty. The *model input* refers to the initial conditions and driving variables. Depending on the input required by a model, this may be the soil, forest stand or climate data but also economic conditions such as market prices or management strategies or simply the format of the data. For example, the grid cell size of the input data influenced NPP predictions of forest ecosystem and biosphere models (Jenkins et al. 1999). Uncertainties related to the model input are henceforth referred to as input uncertainty. The *model parameters* are usually fixed values, should have a meaning and should be measureable. Individual parameters can have a strong influence on the results. Jones et al. (2003) for example, showed that projections of future carbon dioxide (CO_2) levels in a coupled climate carbon-cycle GCM are very sensitive to one parameter that governs the response of soil respiration to temperature. Uncertainties related to the model parameters are henceforth

referred to as parameter uncertainty and can be expressed by a distribution of parameter values rather than by a single value. The different locations of uncertainty have different levels of uncertainty and different natures of uncertainty.

Levels of uncertainty

At each location of uncertainty there maybe statistical and scenario uncertainty and uncertainty due to recognized and total ignorance (Walker et al. 2003). Statistical uncertainty refers to the measurement uncertainty, hence sampling error, inaccuracy and imprecision. Scenario uncertainty deals with plausible changes which are based on assumptions and not (easily) verifiable. The uncertainty due to recognized ignorance relates to a lack of knowledge about the system which maybe reducible or irreducible. Finally, uncertainty due to total ignorance refers to the 'unknown unknowns', hence to issues we are not even aware of that we are not aware of. The different levels of uncertainty for one exemplary location of uncertainty are represented by the vertical error bars in Fig. 1-1.

Nature of uncertainty

At each location of uncertainty and for the different levels of uncertainty, there may also be two different natures of uncertainty: epistemic and variability uncertainty (Walker et al. 2003). Epistemic uncertainty refers to uncertainty because of imperfect knowledge while variability uncertainty refers to uncertainty because of natural, human behavioral, social, economic, cultural and technological variability. The different natures of uncertainty for one exemplary location of uncertainty are represented by the horizontal error bars in Fig. 1-1.

A simple example of different dimensions and types of uncertainty

Since these dimensions and types of uncertainties are strongly related to each other and not always equally important and evident, I here apply this classification to maximum tree age as an important model parameter in forest gap models (Bugmann 2001): Since maximum tree age is a model parameter, the location of the uncertainty is naturally in the model parameters. The current value for the maximum age of Scots pine may be 800 years but there will be some uncertainty about that value because of natural variability and because our knowledge is imperfect (i.e. natures of uncertainty). If we have measured Scots pine trees with an appropriate sample size etc., we know that the maximum age will vary by e.g. +/-50 years around the 800 years (i.e. statistical uncertainty), however also this range itself may be subject to natural variability and imperfect knowledge. We can now assume from

physiological knowledge that it is plausible that there should also be trees that have a higher age and thus maximum tree age could also be 100 years higher than the 800 years (i.e. scenario uncertainty). Again this range will be subject to uncertainty due to natural variability and also due to imperfect knowledge. We can now hypothesize that there may be older trees although we do not have any physiological evidence for that (i.e. recognized ignorance) and we can be sure that there will be some natural variability around that range as well as that this knowledge, even if we had it, would be imperfect. Finally, we simply do not know what the maximum age is, was and will be and thus we will never know how the full range of uncertainty looks like (i.e. total ignorance) and even then there would be an uncertainty about that range due to natural variability and imperfect knowledge.

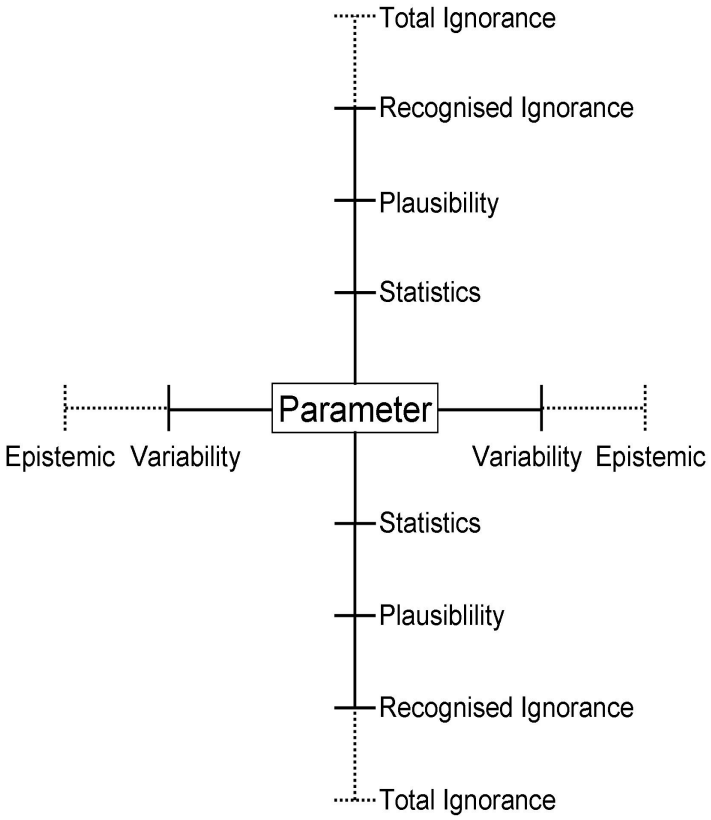

Fig. 1-1: The different levels and natures of uncertainty at one exemplary location of uncertainty, (i.e. model parameters). The different levels and natures of uncertainty are exemplified as vertical (levels) and horizontal (natures) 'error bars'. The dotted lines represent uncertainties that can never be fully addressed. For further explanations see the description in the text.

1.2.2 The cascade of uncertainties

In climate change impact assessments, all the above mentioned uncertainties exist at the different points of the assessment and create a cascade of uncertainties (Henderson-Sellers 1993; Jones 2000; Ahmad et al. 2001; Olesen et al. 2007; Wilby & Dessai 2010). Fig. 1-2 presents a representation of such a cascade of uncertainties for climate change impacts on

forests and subsequent policy and management decisions and also highlights the different dimensions of uncertainty at each stage of the cascade.

Since anthropogenic climate change is mostly driven by an increase in the atmospheric concentration of greenhouse gases, usually in a first step assumptions about the development pathways of future societies have to be made. The most well-known examples of development pathways are the different storylines of the IPCC's Special Report on Emission Scenarios (SRES, Nakicenovic et al. 2000). These storylines are then fed into Integrated Assessment Models (IAMs) which project the greenhouse gas emissions associated with each development storyline. It is important to note that recently the SRES scenarios have been replaced by so-called Representative Concentration Pathways (RCPs) for the Fifth Assessment Report of the IPCC (Moss et al. 2010; van Vuuren et al. 2011, see the Appendix to chapter 1 for a more complete description). The greenhouse gas emissions then drive GCMs to provide global climate change scenarios, usually on a 0.5° grid. For regional applications, the GCM results are then downscaled to lower resolutions (typically 0.2°) using RCMs. To use that data at the forest stand level, a further downscaling/interpolation to the points at which particular forest stands will be simulated is required. After the interpolation/downscaling, the data may be used as input into a forest model. The results of the forest model can then be fed into decision support systems or other toolboxes and models that support decision-making in forest management and policy.

Quantifying uncertainties at specific points in the cascade of uncertainty has been subject to research for a long time. Visser et al. (2000) for example tried to differentiate which sources of uncertainty are of crucial and which of less importance in global temperature projections. Lower in the cascade of uncertainties, several studies assessed parameter uncertainty of forest carbon models using Monte Carlo simulations (e.g. van der Voet & Mohren 1994; Heath & Smith 2000; French et al. 2004). However, only rarely, the effects of the assessments of one dimension and types of uncertainty are combined with assessments of other dimensions. There are however powerful methods to quantify uncertainties (van Oijen et al. 2005) and the necessary data and computational power is increasingly available. Thus prospects for decreasing uncertainty in the future are good. However, with increasing knowledge, available information and more stringent testing methods, some types of uncertainties may even increase (Walker et al. 2003). An example for the latter is that an improved understanding of climate processes leads to larger uncertainty ranges of climate projections (Maslin & Austin 2012).

Even if knowledge is lacking or disputed, there are ways to address uncertainties. There is for example recognized ignorance about the physiological effect of CO_2 on tree growth (Körner 2006). This can be partly addressed by making plausible assumptions in model experiments about the effects of CO_2, for example by testing the effect of persistent CO_2-effects versus a leveling-off of CO_2-effects when plant photosynthesis is acclimatizing or limited by other factors.

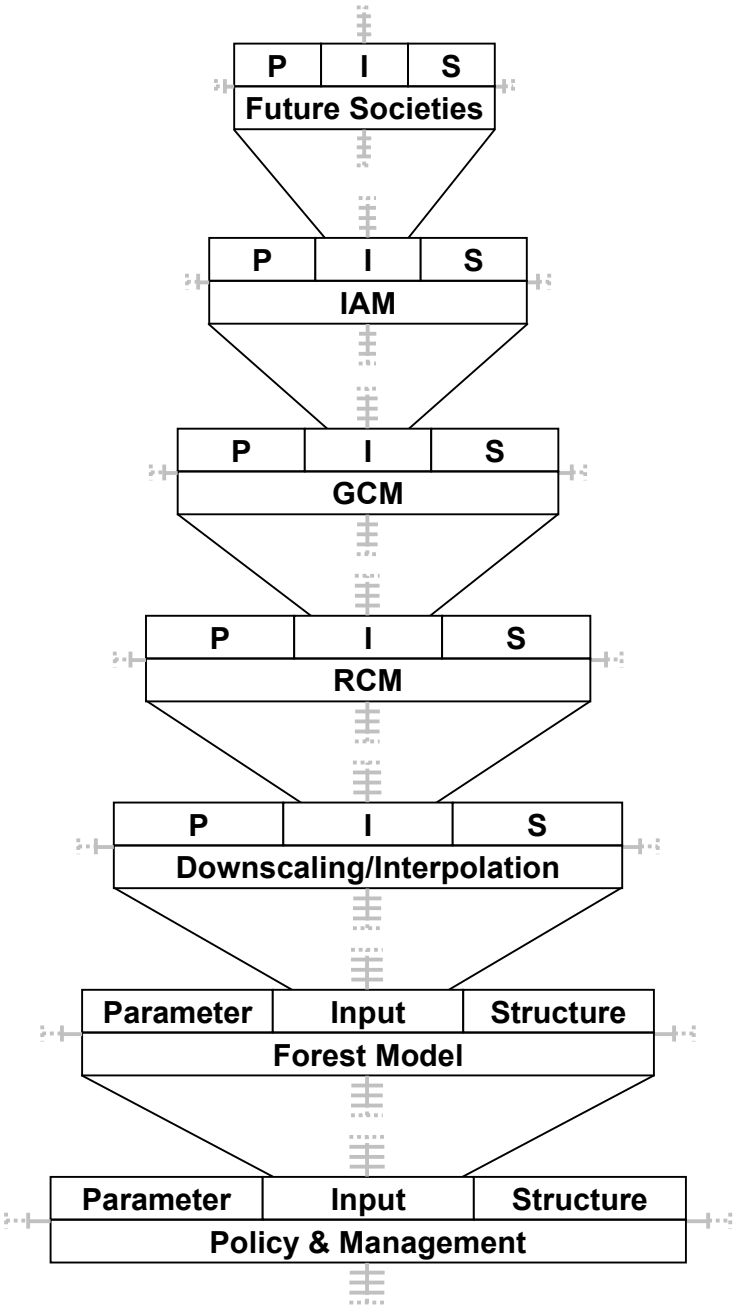

Fig. 1-2 The cascade of uncertainty. The upper boxes of each compartment represent three locations of uncertainties common to every step of the cascade and the stylized error bars the levels and natures of uncertainty.

1.3 Objectives and research questions

The main objective of this thesis is to address the cascade of uncertainty in environmental change studies in a structured way at the example of forest ecosystems. This leads to two overarching research questions:

1. How do different types of uncertainties affect projections of the effects of environmental change on forest ecosystems?
2. What is the general framework of sustainable natural resource management in coupled social-ecological systems in which uncertainties need to be integrated?

The overall objective as well as the two research questions will be broken down in more specific questions addressed in each chapter:

The objective of chapter 2 is to provide a synthesis of process-based, stand-scale model predictions of changes in forest carbon and biomass pools and fluxes under climate change, elevated CO_2 and nitrogen deposition. Chapter 2 deals primarily with model structural uncertainty and addresses the following research questions:

1. Which regions, forest types and environmental drivers are mostly considered in studies of process-based, stand-scale model predictions of changes in forest carbon and biomass pools?
2. Which are the responses to environmental change in different biomes, to different environmental drivers separately and in combination and to different warming rates?
3. What is the uncertainty range of these responses?

The objective of chapter 3 is to assess productivity shifts in Europe under various climate change scenarios and elevated CO_2 using the process-based forest model 4C. Chapter 3 deals with model input uncertainty and addresses the following research question:

1. What is the influence of a large range of climate change scenarios on forest net primary productivity in the 21st century?

The objective of chapter 4 is to integrate parameter uncertainty into simulations of climate change impacts on forest productivity using the process-based forest model 4C. Chapter 4 deals primarily with model parameter uncertainty and addresses the following research question:

1. How do the effects of input uncertainty arising from using several climate change scenarios compare with the effects of both input and parameter uncertainty?

The objective of chapter 5 is to compare several European forest models before and after Bayesian calibration in four European countries and to quantify the uncertainty of their predictions. Chapter 5 deals with model structural and parameter uncertainty and addresses the following research questions:

1. How effective are local stand data in reducing uncertainties about forest model parameters in a Bayesian framework?
2. Are the considered dynamic models for Scots pine sufficiently general to allow a generic calibration to data from across Europe, or should models be calibrated on a country-by-country basis?
3. How effective is Bayesian model comparison in identifying plausible predictive models, and what are the main distinguishing characteristics of forest models that are selected?
4. Does Bayesian model averaging lead to improved predictions compared to individually calibrated models?

The objective of chapter 6 is to review the effects of climatic variability on plants at different scales. Chapter 6 deals with model structural uncertainties and addresses the following research questions:

1. Which plant processes are vulnerable to changes in the variability of climatic drivers rather than to changes in their mean?
2. How can we quantify responses of plants to changing climatic variability?

The objective of chapter 7 is to provide an integrated analysis of climate change adaptation measures in four sectors in a sustainable development framework. Chapter 7 deals with the overall context in which the results of the preceding chapters have to be interpreted in and addresses the following research question:

1. What are the appropriate strategies for adapting Brandenburg to the various and partly uncertain impacts of complexly related global changes?

1.4 Structure of the thesis

This thesis consists of a set of stand-alone scientific articles that are either published (chapters 5, 6 and 7), submitted for publication (chapters 3 and 4) or close to being submitted (chapter 2). Each chapter addresses different aspects of the cascade of uncertainty in forest modeling (Fig. 1-3). The chapters 2 to 4 are directly related to modeling the effects of different components of environmental change on forests. Chapter 2 is a review of existing modeling studies and hence relates mostly to model structural uncertainties. The chapters 3 and 4 are applications of the process-based model 4C considering input (chapter 3) or parameter uncertainty (chapter 4). Chapter 5 is not directly related to the impacts of environmental change but rather a description of how to use available data-assimilation methods and forest inventory data to assess model structural and parameter uncertainty. These techniques are the basis for assessing the impacts of environmental change as exemplified in chapter 4. Chapter 6 provides a general overview of how one specific aspect of climate change, namely climatic variability, affects plants and how climatic variability can be assessed in different study designs. It thus mostly relates to model structural uncertainty. Chapter 7 does not relate to forest ecosystem modeling but rather has the character of an outlook chapter. It provides an overview of the general framework in which the information generated in the previous chapters has to be integrated to enhance the sustainable management of natural resources and foster sustainable development of rural regions.

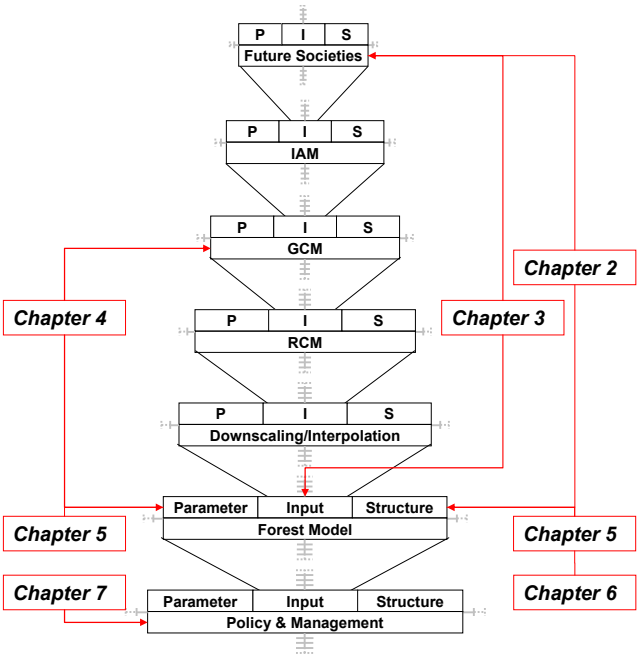

Fig. 1-3 Structure of the thesis. The red lines indicate which aspects of uncertainty are addressed and which parts of the cascade of uncertainty are covered by the individual chapters. For explications of the cascade of uncertainty see Fig. 1-2 and the text.

1.5 Author's contribution to the chapters of the thesis

1.5.1 Chapter 2

I developed the idea for a quantitative review of climate change projections of stand-scale, process-based models. I was entirely responsible for developing the concept, investigating the literature, programming the data analysis scripts, analyzing the data and writing the manuscript. The whole process was supervised by and discussed with Petra Lasch-Born. Martin Gutsch helped with parts of the analysis.

1.5.2 Chapter 3

The idea for an application of 4C across Europe was developed within the framework of the MOTIVE project. I contributed predominantly to refining and operationalising this idea and developed the research and simulation concept with Petra Lasch-Born and Felicitas Suckow. I investigated the literature, analyzed the data and wrote the manuscript with inputs from the co-authors. I was also strongly involved in the development of the methods and the preparation of the input data with support of the co-authors.

1.5.3 Chapter 4

I developed the idea of assessing parameter uncertainty and climate change uncertainty in one joint analysis. I was responsible for developing the concept, investigating the literature, designing the simulation concept, preparing the input data, carrying out the model runs, programming the post-processing and analysis scripts, analyzing the data and writing the manuscript. My co-authors commented on the manuscript and the data evaluation. The general methodological approach was the same as developed in the paper presented in chapter 5 and was supported by my co-authors.

1.5.4 Chapter 5

The idea for this paper was developed during two workshops of working group 3 of the COST Action FP0603. I was involved in developing the concept and I prepared the input data for all modeling groups. Together with Petra Lasch-Born and Michael Flechsig, I implemented the Bayesian calibration for 4C and programmed the Markov Chain Monte Carlo algorithm. Furthermore, I performed the 4C runs, programmed the post-processing scripts for 4C and contributed to the writing of the manuscript.

1.5.5 Chapter 6

This paper builds upon a session I convened together with Sebastian Leuzinger, Anja Rammig and Annett Wolf at the general assembly of the European Geosciences Union in the year 2011. After the session, Sebastian Leuzinger and I developed the concept for the manuscript. I led the investigation of the literature, coordinated the inputs from the co-authors and wrote the manuscript with input from all co-authors.

1.5.6 Chapter 7

I developed the concept for this paper and wrote the theoretical part of the paper as well as the forestry section with comments from my co-authors. I also coordinated the contributions to the water management, agriculture and nature conservation sections. Finally, I developed the integrative perspective of the sectoral sections and developed the figures and tables with the support of my co-authors.

2 Projections of changes in forest productivity and carbon pools under environmental change – A review of modeling studies[1]

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[1] This chapter is in preparation to be submitted to *Global Change Biology*.

Abstract

Climate change, increasing atmospheric CO_2 concentrations, nitrogen deposition and recovery from past management have lead to changes in forest productivity and carbon pools. Process-based forest models have been widely used to project such changes under changing environmental conditions into the future. Based on a review of published simulation results from a large number of process-based models, we present a synthesis of stand-scale impacts of environmental change on forest productivity and carbon pools and associated uncertainties. We show that there are biases of stand-scale process-based model studies towards temperate and boreal forests, towards mostly mono-specific forests with a focus on tree species that are relevant for forestry and towards analyses of climate change and increasing CO_2 rather than other environmental drivers. Forest productivity and carbon pools mainly respond positively to environmental change especially if the effects of increasing CO_2 are included. However, if climate change is considered in isolation, 35% of the simulations show decreasing forest productivity and declining carbon and biomass stocks. Although our results have large uncertainty ranges due to the wide range of environmental change scenarios, model structures, data sets and time frames covered, the overall responses we find transcend this variability: Boreal forest mostly become more productive and sequester more carbon under climate change and increasing CO_2, while temperate and especially Mediterranean forests show more ambivalent responses depending on the importance of individual environmental driving variables. We find that the positive physiological response (i.e. without considering altered disturbance regimes) of forest productivity and carbon pools to climate change and increasing CO_2 culminates at a decadal warming rate of 0.4-0.5K and declines at higher rates. Future modeling studies should increasingly strive to incorporate mixed stands, tropical forests and other environmental drivers besides climate and CO_2 to better capture future changes in forest productivity and carbon pools.

Keywords: Carbon dioxide, Climate change, Forest stand scale, Literature synthesis, Modeling, Nitrogen, Ozone, Process-based models

2.1 Introduction

In past decades, ground-based measurements and satellite data have indicated shifts in forest productivity and carbon pools in all major biomes (Kauppi et al. 1992; Myneni et al. 1997; Phillips et al. 1998; Nemani et al. 2003; Feeley et al. 2007; Lewis et al. 2009; McMahon et al. 2010). These observations have been attributed to environmental change such as increasing nitrogen deposition, increasing atmospheric CO_2 concentrations and climate change but also to changing management practices (e.g. Spiecker et al. 1996; Boisvenue & Running 2006). Recent analyses have shown that nitrogen depositions indeed have a fertilizing effect on forest productivity and increase carbon sequestration (de Vries et al. 2006, 2009; Solberg et al. 2009). Increasing CO_2 affects productivity by enhancing photosynthesis and water use (Körner 2006; Leuzinger & Körner 2007). Climate controls productivity of forests throughout the world as evidenced by analysis of dendrochronological (e.g. Lebourgeois et al. 2005), observational (Solberg et al. 2009; Stegen et al. 2011), flux (Yi et al. 2010) and satellite (Nemani et al. 2003; Zhao & Running 2010) data. Increasing temperatures directly affect tree productivity through its effects on growth temperatures (Way & Oren 2010) and indirectly in combination with precipitation through its effects on growing season length (Wang et al. 2011; Jeong et al. 2011) and soil water status. All these environmental factors interact (also with other environmental variables such as ozone (O_3)) in complex and multiple ways (Kirschbaum 2000; Aber et al. 2001) and vary regionally. Abe*r* et al. (2001), Hyvönen et al. (2007) and Chmura et al. (2011) present more detailed reviews of the effects of environmental change on forest processes. It is crucial for many forest services such as carbon sequestration as well as for forests' adaptation to climate change to determine how forest productivity and carbon pools will change under projections of future environmental change.

Besides studying observable effects of environmental change on forest productivity and carbon pools at long-term monitoring sites, models can be used to analyze and predict forest productivity and carbon pools under environmental change. An advantage of models is that, by integrating knowledge from observations and experiments, they allow for generating and testing hypotheses, including many environmental drivers and analyzing influences of individual drivers over long time periods and under different environmental change scenarios. However, this flexibility comes at the cost of simplifying the system to a degree that essential responses and feedbacks maybe lost. Furthermore, model-based projections of the effects of environmental change suffer from several types of uncertainties (e.g. Buisson et al. 2010). Firstly, *input uncertainty* reflects how results depend on the input data

that is used to drive a model. Secondly, *model parameter uncertainty* refers to a variety of possible parameter values. Thirdly, *model structural uncertainty* refers to the inclusion of or the representations of different model processes. All these uncertainties need to be accounted for when interpreting the results of model projections (Cipra 2000). An important part of this is to estimate uncertainty ranges of projections of future forest productivity and carbon pools.

There are many model types that have been used for simulating the impacts of changing environmental conditions on forests (Medlyn et al. 2011) and much progress has been made since Agren et al. (1991)'s and Shugart et al. (1992)'s early reviews of such models. Gap-type models (see review by Bugmann 2001) capture long-term forest dynamics but have been criticized for oversimplifying tree growth responses to climate (Schenk 1996; Loehle & LeBlanc 1996). Purely empirical models that rely on statistical relationships can not be extrapolated to novel environmental conditions which were not used for model fitting. Process-based models (PBMs) are most suitable for environmental change studies since they combine changes in environmental variables with plant responses to this change in a mechanistic way (Mäkelä et al. 2000; Landsberg 2003; Fontes et al. 2010). Stand-scale PBMs simulate the impact of environmental drivers on forest stands and provide detailed physiological and structural output. They require detailed input data for model initialization (Fontes et al. 2010) and their usually species-specific parameters are derived from physiological measurements (Landsberg 2003). This level of detail differentiates them from process-based dynamic global vegetation models or global biogeochemical models that simulate global or regional responses to environmental change for plant functional types (Betts & Shugart 2005).

Stand-scale PBMs thus represent system dynamics and processes at spatial and (to a limited extent) temporal scales similar to observational studies (e.g. eddy-covariance flux towers or intensive monitoring plots) which are being used to study past and current impacts of environmental change on productivity (see review by Boisvenue & Running 2006). It is important to emphasize that they represent physiological responses to environmental drivers at the local scale and only seldom integrate processes that occur at the landscape scale such as disturbances (e.g. storms or insect outbreaks). Although they work at similar spatial scales and include similar processes (e.g. photosynthesis, allocation etc.), the level of detail in process description, the temporal resolution and the coupling of processes differ. PBMs can be used either as diagnostic tools to disentangle the importance of individual environmental drivers on forest productivity in the past (e.g. Ollinger et al. 2002; Pan et al.

2009; Eastaugh et al. 2011) or to generate projections of future forest productivity and carbon pools under environmental change. The latter can also be carried out in an experimental set-up by varying environmental drivers individually and in combinations (e.g. Su et al. 2007). While such an approach enables an assessment of the relative contribution of environmental drivers to the model result, simulations combining important drivers represent the most comprehensive assessments of environmental change on forests. The change in environmental drivers can be gradual, simulating transient change (e.g. Kellomäki & Väisänen 1997), or stepwise (e.g. Kramer 1995). Thus, even within this narrowly defined model type of stand-scale PBMs, there is a broad variety of approaches towards simulating forest productivity and carbon pools under environmental change.

Therefore, synthesizing the results of different stand-scale PBMs provides an assessment of changes in forest productivity and carbon pools under changing environmental conditions. Furthermore, summarizing the results of several models allows evaluating if model results are consistent across different model structures. Hence, the objectives of this paper are (1) to review published stand-scale process-based model projections of changes in forest productivity and carbon pools driven by environmental change, (2) to synthesize these studies with regard to spatial coverage, studied forest types and environmental drivers considered, (3) to quantify the responses a) in different biomes, b) to different environmental drivers separately and in combination and c) to different warming rates and (4) to display uncertainty ranges of these responses. We do not intend to explain the individual models' results in terms of the underlying processes that are specific for each model nor to judge the models' quality. Although the models have different structures and use different input data we hypothesize that general pattern of changes in forest productivity and carbon pools under environmental change will transcend these methodological differences at higher levels of aggregation.

2.2 Material and methods

2.2.1 Literature search

We aimed at a comprehensive and systematic review of published studies of changes in future forest productivity and carbon pools. To this end, we searched the Web of Science database, with four sets of search terms resulting in 108 different combinations of key words (Fig. 2-1). This large number of search terms spanned a broad range of studies. In November 2011, this search resulted in 7 642 journal articles of which we selected those presenting

projections of future forest productivity and carbon pools by reading the titles and abstracts. The resulting set of about 600 papers was further narrowed down to those studies addressing individual forest stands with process-based models. This excluded gap and hybrid/empirical models. This selection concurs broadly with Medlyn et al. (2011)'s model types 1 and 2 (i.e. stand-scale, process-based models and biogeochemical models) which stresses our focus on mechanistic models applied at the stand scale without considering changing species composition. Another important criterion for the selection of studies was that model output on changes in forest productivity and carbon pools should be available for individual stands. Studies that simulated individual stands but reported only aggregated values for several stands were excluded. If the same set of simulations was used in several papers (e.g. under different viewpoints or response variables), we only considered the main study to avoid double-counting of the same model simulations. We accounted for different versions of the same model by recording the names of different model versions if specified in the publications.

This search resulted in 73 journal articles. While examining them we identified one paper that fulfilled our search criteria but was not detected by our search terms (i.e. McMurtrie & Wang 1993). Thus, our final dataset consisted of 74 papers (Table 2-1) that qualified for a more detailed review and synthesis.

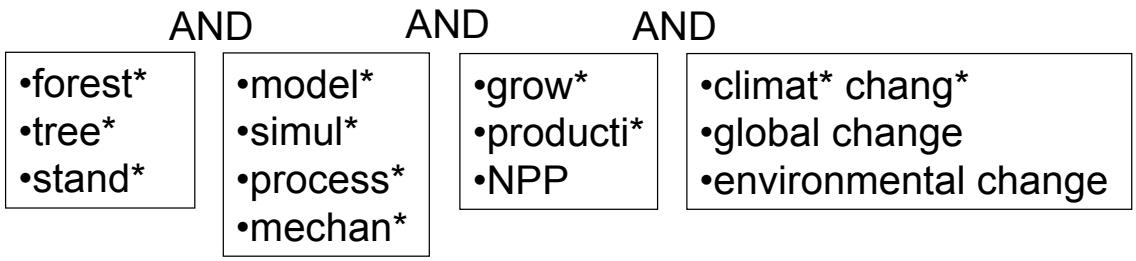

Fig. 2-1 Search terms used in the literature search, yielding 108 combinations of key words.

2.2.2 Data compilation and analysis

Results of individual model simulations described in the papers were the main entity of the analysis. To analyze the papers, we extracted for each simulation general information (coordinates of the simulated stands, simulated species, length of the simulation period, type of change of driving variables (stepwise or transient), model name, and biome), the driving variables (i.e. climate change (consisting of increasing temperature and/or changing precipitation), CO_2, nitrogen, ozone (O_3) and their combinations) and the respective response variable considered in the studies. We recorded response variables that relate to forest biomass and carbon pools (e.g. volume, wood carbon) and to forest productivity (e.g.

stem increment, net primary production (NPP)). Since biomass could be easily converted to carbon, we refer to forest productivity and carbon pools throughout this paper. Some studies only presented relative changes in driving variables and in response variables relative to baseline conditions rather than absolute values. To ensure comparability, we calculated relative changes of driving and response variables for all simulations with respect to the baseline scenario of each study. Hence, we always report and analyze the changes 'relative to baselines conditions' throughout this paper to avoid comparing the absolute values of different response variables but to focus on the changes induced by driving variables. Analyzing different response variables together seems appropriate in this context, since there are relationships between biomass and productivity (Keeling & Phillips 2007, Ciais et al. 2008) and also between various variables of forest productivity (e.g. Pregitzer & Euskirchen 2004). Disturbances as environmental drivers, which strongly affect forest biomass (Pregitzer & Euskirchen 2004) and bias the productivity biomass relationship, were excluded from the analysis because they are only integrated to a very limited degree in stand-scale PBMs (e.g. in Grant et al. 2006). If present, we included results of simulation experiments featuring different management types or intensities under changing environmental conditions but did not analyze them separately from simulations of unmanaged forests. Effects of forest management and age structure can be very important for forest productivity and carbon pools (e.g. in the U.S.A. (Houghton et al. 1999; Caspersen et al. 2000 (but see Joos et al. 2002); Schimel et al. 2000; Drake et al. 2011)). However, they vary regionally and depend to a large extent on socioeconomic developments such as wood prices, agricultural policies and demographic developments. Thus, we simply interpreted different management scenarios as a variation of stand conditions that will still be influenced by changing environmental variables. Moreover, we included simulations results of mixed forests at the individual species-level if these were presented as individual simulations or at the forest-level if one model simulation included several species.

This study focused on the results of individual simulations and hence sample sizes or estimates of variances of the response variables are not available. This precludes more formal statistical meta-analysis methods and techniques (e.g. Gurevitch & Hedges 1993; Dieleman & Janssens 2011) which are common in experimental studies (e.g. Wu et al. 2011).

We structured the analysis in three parts which correspond to subsets of the data that allow analyzing different aspects of the dataset. The first part consists of a *qualitative analysis of all studies found in the literature search*, the second of a *quantitative analysis of simulations driven by transient change in climate and* CO_2 individually as well as their combination and

the third of a subset of the second that contains a *quantitative analysis of simulations combining climate change and CO_2-effects driven by transient change.* In this part of the analysis, we calculated the decadal warming rate of each study (hence the change in temperature over the simulation time) and classified the results into six classes of decadal warming rates ranging from 0.2K to greater than 0.6K.

We used the statistical software R (R Core Development Team 2011) for all statistical analysis. For the calculation of the density functions, we used the standard function of R (package *stats*) to compute kernel density estimates. To analyze the simulations combining climate change and CO_2-effects driven by transient change, we fitted a polynomial function to the median of each class of decadal warming rate. We deliberately used the median and not the mean values due to non-normality of the data and several outliers.

2.3 Results

2.3.1 Qualitative analysis of all studies found in the literature search

The 74 studies reviewed here were almost entirely restricted to the temperate and boreal forests in the northern hemisphere, especially Europe and Northern America (Fig. 2-2a, Table 2-1). Only two studies were found for the Tropics in Asia, none for South-America or Africa. The 74 studies represent 1209 single simulations runs carried out with 55 different models or model versions. More than 50% of the simulations looked at the coniferous genera Pinus (30%) and Picea (22%). The broad-leaved genera Betula (12%), Fagus (9%) and Quercus (7%) made up almost another third of the simulations. Most of the studies assumed a changing climate (temperature and/or precipitation) and/or increasing CO_2 but only few considered changes in nitrogen deposition and ozone (Table 2-1). Roughly 56% of the simulations analyzed the effect of stepwise changes of environmental change drivers in their scenarios, whereas the remaining simulations featured transient responses (44%).

The direction of change of the response to environmental change was positive for 79%, negative for 19% and none for 2% of the simulations (Table 2-1). The proportion of positive and negative response per studied site shows a distinct geographical pattern. For most studies in the boreal forests the responses are positive whereas the response is ambivalent in temperate and Mediterranean forests (Fig. 2-2a). There were 333 simulations which considered a changing climate (i.e. increasing temperatures and changing precipitation) without changes in CO_2. Thereof, 61% showed positive, 35% negative and 3% no changes

(Fig. 2-2c). A greater number of simulations (870) had been run with a changing climate and increasing CO_2. Here, 87% of the simulations were positive, 12% negative and 1% not changing (Fig. 2-2b). Only six simulation runs did not consider climate change or increasing CO_2 at all but the effects of nitrogen (five simulations with positive responses) and ozone (one simulation with negative responses) individually. The remaining simulations including nitrogen and ozone as driving variables were always confounded with climate change and/or CO_2 scenarios.

Table 2-1 Summary of changes in forest productivity and carbon pools as simulated by stand-scale process-based models. The studies are differentiated whether their response variables relate to forest productivity or to carbon pools. The section on carbon pools also includes biomass pools since these could be converted into carbon. NEP = Net Ecosystem Production, NPP = Net Primary Productivity, GPP = Gross Primary Productivity, NEE = Net Ecosystem Exchange, CAI = Current Annual Increment, MAI = Mean Annual Increment, CO_2 = atmospheric CO_2-concentration, T = temperature, P = Precipitation, N = Nitrogen, O_3 = Ozone, * = stepwise, ' = transient without specifying future period, na = information could not be derived from the paper.

Response variable	Response					Time Scale	Model	Biome	Country/ Region	Scenarios	Source
	Overall	Negative	Positive	Zero	Total						
Productivity											
NPP (aboveground)	minus	10	0	0	10	na*	PnET	Boreal, Temperate	USA	P+T	Aber & Federer 1992
NPP	plus	0	3	0	3	10*	SDGVM	Boreal	Norway	CO_2, T, CO_2+T	Beerling et al. 1997
NPP	plus/minus	2	28	0	30	3*	BIOMASS	Boreal	Europe	CO_2, T, CO_2+T	Bergh et al. 2003
NPP	plus	0	6	0	6	100*	SIMFORG-SICA	Boreal, Temperate, Mediterranean	Europe	CO_2+T	Berninger & Nikinmaa 1997
GPP	plus	0	12	0	12	na*	SICA	Boreal, Temperate, Mediterranean	Europe	CO_2+T, CO_2+P+T	Berninger 1997
NPP	plus/minus	1	17	0	18	1950-2089'	BIOME-BGC	Temperate	USA	CO_2+N+P+T	Boisvenue & Running 2010
Volume Increment	plus/minus	2	49	0	51	10*	CenW	Tropics (plantation)	Vietnam	CO_2, P+T, CO_2+P+T	Booth et al. 1999
NPP	plus	0	4	0	4	2000-2100'	PnET-BGC	Temperate	USA	P+T	Campbell et al. 2009
NPP	plus/null	0	5	1	6	1990-2050'	Hybrid	Temperate	UK	CO_2, N, T, CO_2+N, CO_2+T, CO_2+N+T	Cannell et al. 1998
NPP	plus	0	6	0	6	1990-2050'	ITE-EFM	Temperate	UK	CO_2, N, T, CO_2+N, CO_2+T, CO_2+N+T	Cannell et al. 1998
Yield	plus	0	1	0	1	150*	SECRETS	Temperate	Belgium	CO_2+P+T	Deckmyn et al. 2004
NPP (stem)	plus	0	4	0	4	2040-2060'	StandLEAP-v0v6	Boreal	Canada	P+T	Girardin et al. 2008
NPP	plus	0	1	0	1	70'	ecosys	Boreal	Canada	CO_2+P+T	Grant & Nalder 2000
NPP	plus	0	1	0	1	150'	ecosys	Boreal	Canada	CO_2+P+T	Grant et al. 2001b
NEP	plus/minus	2	10	0	12	3*	ecosys	Boreal	Canada	T	Grant et al. 2009
NEE	plus/minus/null	5	3	1	9	11*	INTRASTAND	Temperate	USA	CO_2, O_3, P, T, CO_2+P+O_3+T	Hanson et al. 2005
Increment (stem)	plus/minus	16	5	0	21	1961-2100'	BIOME-BGC	Temperate	Slovakia	CO_2+N+P+T	Hlásny et al. 2011
NPP	plus	0	3	0	3	2008-2050'	VISIT	Boreal, Temperate	Japan	CO_2+T	Ito 2010
NEE	plus	0	8	0	8	100'	CoupModel	Boreal	Sweden	P+T	Jansson et al. 2008
GPP	plus/minus	11	3	0	14	1*	PERUN_3	Temperate	Slovenia	CO_2, T, CO_2+T	Kajfez-Bogataj & Hocevar 1994
Production (stemwood)	plus/null	0	8	2	10	76-100'	FINNFOR	Boreal	Finland	CO_2, P, T, P+T, CO_2+P+T	Kellomäki et al. 1997
CAI (stemwood)	plus	0	4	0	4	1950-2030'	CenW-1.0.5	Temperate	Australia	CO_2+T, CO_2+N+T, CO_2+P+T, CO_2+N+P+T	Kirschbaum 1999
CAI (stemwood)	plus	0	4	0	4	50'	CenW-1.0.5	Temperate	Australia	CO_2, CO_2+N, CO_2+P, CO_2+N+P	Kirschbaum 1999
CAI (stemwood)	plus	0	11	0	11	20*	CenW-1.0.5	Temperate	Australia	CO_2, N, P, T, CO_2+N, CO_2+P, N+P, P+T, CO_2+N+P, N+P+T	Kirschbaum 1999
NPP	plus/minus	6	5	1	12	100*	FORGRO	Temperate	The Netherlands	CO_2+P+T	Kramer & Mohren 1996
NPP	plus/null	0	11	1	12	100'	FORGRO	Temperate	The Netherlands	CO_2+P+T	Kramer & Mohren 1996
Gross Photosynthesis	plus/minus	6	18	0	24	14*	FORGRO	Temperate	The Netherlands	CO_2, CO_2+T	Kramer 1995
Gross Photosynthesis	plus	0	24	0	24	14*	FORGRO-PGEN	Temperate	The Netherlands	CO_2, CO_2+T	Kramer 1995
Gross	plus/minus	5	17	2	24	14*	ITE-FORGRO	Temperate	The Netherlands	CO_2, CO_2+T	Kramer 1995

Response variable	Response					Time Scale	Model	Biome	Country/ Region	Scenarios	Source
	Overall	Negative	Positive	Zero	Total						
Photosynthesis NPP	plus/minus	31	65	0	96	50*	FORGRO	Temperate	The Netherlands	CO_2, CO_2+T	Kramer et al. 1996
Net photosynthesis	plus/minus/null	5	42	1	48	1*	MAESTRO	Temperate	Scotland	CO_2, T, CO_2+physiological adjustments, T+physiological adjustments, CO_2+T+physiological adjustments	Kruijt et al. 1999
MAI	plus/minus/null	22	25	1	48	2041-2070'	4C	Temperate	Germany	P+T	Lasch et al. 2002
Net Photosynthesis	plus/minus/null	1	4	1	6	90*	OAKWBAL	Temperate	USA	T	Leblanc & Foster 1992
NPP	plus	0	2	0	2	2000-2050/2100'	FORGRO-phen	Boreal	Scandinavia	T	Leinonen & Kramer 2002
NPP	plus	0	1	0	1	24*	FORDYN	Temperate	USA	CO_2	Luan et al. 1999
NPP	plus	0	8	0	8	10*	FORDYN	Temperate	USA	CO_2	Luan et al. 1999
Carbon Sequestration	minus	2	0	0	2	1987-2085*	TGS	Temperate	USA	CO_2	Luo & Reynolds 1999
Carbon Sequestration	plus	0	2	0	2	1987-2085'	TGS	Temperate	USA	CO_2	Luo & Reynolds 1999
NPP	plus/null	0	46	2	48	na*	BIOME-BGC	Tropical	China	CO_2, CO_2+T	Luo et al. 2010
GPP	plus	0	6	0	6	1*	SPA	Temperate	Australia	CO_2+physiological adjustments	Macinnis-Ng et al. 2010
NEE	plus/minus	2	13	1	16	range 1990-2095'	HYDRALL	Mediterranean	Italy	CO_2+P+T	Magnani et al. 2004
NPP	plus	0	4	0	4	300*	G'DAY	Temperate	Australia	CO_2	McMurtrie & Comins 1996
Canopy Carbon Gain	plus/minus	1	2	0	3	1*	BIOMASS	Temperate	Australia	CO_2, T, CO_2+T	McMurtrie & Wang 1993
Canopy Carbon Gain	plus/minus	1	1	0	2	8*	BIOMASS	Temperate	Australia	CO_2, T	McMurtrie & Wang 1993
NPP	plus	0	1	0	1	100'	G'DAY	Boreal	Sweden	T	McMurtrie et al. 2001
NPP	plus	0	4	0	4	100*	G'DAY	Boreal	Sweden	N, T	McMurtrie et al. 2001
NPP	plus/minus	19	5	0	24	40*	PnET-IIS	Temperate	USA	P, T, P+T	McNulty et al. 1996
NPP	plus	0	11	0	11	100*	G'DAY	Boreal, Temperate	Australia	CO_2, T, CO_2+T	Medlyn et al. 2000
NPP	plus/minus	1	26	0	27	100'	Century-4.0	Boreal	Canada	CO_2, P+T, CO_2+P+T	Peng & Apps 1998
NPP	plus/minus	1	26	0	27	100'	Century-4.0	Boreal	Canada	CO_2, P+T, CO_2+P+T	Peng & Apps 1999
NPP	plus	0	5	0	5	1996-2100'	G'DAY	Boreal	Sweden	CO_2, T, CO_2+N, CO_2+T, CO_2+N+T	Pepper et al. 2005
NPP	plus/minus	1	4	0	5	1996-2100'	DAYCENT	Boreal	Sweden	CO_2, T, CO_2+N, CO_2+T, CO_2+N+T	Pepper et al. 2005
NPP	plus/minus	2	2	0	4	1*	BEPS	Boreal	Canada	CO_2, P, T	Potter et al. 2001
NPP	plus/minus/null	1	1	2	4	1*	BGC	Boreal	Canada	CO_2, P, T	Potter et al. 2001
NPP	plus/minus/null	1	1	1	3	1*	NASA-CASA	Boreal	Canada	P, T	Potter et al. 2001
NPP	plus/minus	1	3	0	4	1*	CLASS	Boreal	Canada	CO_2, P, T	Potter et al. 2001
NPP	plus	0	4	0	4	1*	ecosys	Boreal	Canada	CO_2, P, T	Potter et al. 2001
NPP	plus/minus	3	1	0	4	1*	FORFLUX	Boreal	Canada	CO_2, P, T	Potter et al. 2001
NPP	plus/minus/null	2	1	1	4	1*	Lotec	Boreal	Canada	CO_2, P, T	Potter et al. 2001
NPP	plus/minus	2	1	0	3	1*	SPAM	Boreal	Canada	P, T	Potter et al. 2001
NPP	plus	0	4	0	4	1*	TEM	Boreal	Canada	CO_2, P, T	Potter et al. 2001
NPP (aboveground)	plus	0	45	0	45	30/31*	BIOME3C	Mediterranean	France	CO_2, P+T, CO_2+P+T	Rathgeber et al. 2003
NPP	plus	0	4	0	4	2000-2044'	4C	Temperate	Germany	CO_2+P+T	Reyer et al. 2010
NPP	plus	0	18	0	18	1960-2049/2099'	GOTILWA+	Mediterranean	Italy, Spain	CO_2+P+T	Sabaté et al. 2002

Response variable	Response					Time Scale	Model	Biome	Country/ Region	Scenarios	Source
	Overall	Negative	Positive	Zero	Total						
Forest Carbon Production	plus	0	6	0	6	1994-2100'	Century-4.5	Temperate	USA	P+T	Smithwick et al. 2009
NPP	plus/minus	1	7	0	8	8*	BIOME-BGC	Temperate	China	P, T, CO_2+P, P+T, CO_2+P+T	Su & Sang 2004
NPP	plus/minus	1	27	0	28	40*	BIOME-BGC	Boreal	China	P, T, CO_2+P, P+T, CO_2+P+T	Su et al. 2007
NPP (wood+leaf+root)	plus	0	1	0	1	10*	PnET-II	Temperate	USA	P+T	Sun et al. 2000
NPP	plus/minus	1	7	0	8	60/120'	ITE-EFM	Temperate	UK	T, CO_2+N, CO_2+N+T	Thornley & Cannell 1996
NPP	plus	0	7	0	7	2005-2062'	BIOME-BGC	Boreal	USA	CO_2, T, CO_2+T, P+T, CO_2+P+T	Ueyama et al. 2009
Net photosynthesis	plus	0	1	0	1	1*	Vitale *et al.* 2003	Mediterranean	Italy	T	Vitale et al. 2003
NPP	plus	0	3	0	3	3*	BIOMASS	Boreal	Norway	CO_2, T, CO_2+T	Zheng et al. 2002
Overall productivity											
Total		168	718	18	904						
Pools											
Total Yield (timber)	plus	0	96	0	96	100'	FINNFOR	Boreal	Finland	CO_2+P+T	Briceno-Elizondo et al. 2006
Total Carbon (above+belowground)	plus/null	0	35	1	36	2000-2100'	FINNFOR	Boreal	Finland	CO_2+P+T	Garcia-Gonzalo et al. 2007
Volume (stem)	minus	3	0	0	3	2000-2099'	FINNFOR	Boreal	Finland	CO_2+P+T	Ge et al. 2010
Stem Wood	plus/minus	4	8	0	12	2000-2099'	FINNFOR	Boreal	Finland	CO_2+P+T	Ge et al. 2011
Carbon (wood)	plus	0	2	0	2	150'	ecosys	Boreal	Canada	CO_2+P+T, CO_2+N+P+T	Grant et al. 2001a
Carbon (wood)	plus	0	2	0	2	100'	ecosys	Boreal	Canada	CO_2+P+T	Grant et al. 2006
Carbon (wood)	plus	0	2	0	2	126'	ecosys	Boreal	Canada	CO_2+N+P+T	Grant et al. 2007
Total production (stem)	plus	0	6	0	6	100'	FINNFOR	Boreal	Finland	CO_2, P+T, CO_2+P+T	Kellomäki & Väisänen 1997
Total (wood)	plus	0	6	0	6	200*	CenW-3.0	Temperate	Australia	CO_2	Kirschbaum 2005
Biomass (stem)	plus/minus	3	7	0	10	50'	FORGRO-phen	Boreal, Mediterranean	Finland, France	CO_2, T, CO_2+T, CO_2+P+T	Kramer et al. 2000
Carbon (stem+foliage)	plus/minus	5	2	0	7	100*	Century-4.0	Boreal	Canada	CO_2, P, T, CO_2+P, P+T, CO_2+P+T	Luckai & Larocque 2002
Carbon (stem+foliage)	plus/minus	2	5	0	7	100*	Forest-BGC	Boreal	Canada	CO_2, P, T, CO_2+P, P+T, CO_2+P+T	Luckai & Larocque 2002
Total Yield	plus	0	6	0	6	100'	FINNFOR	Boreal	Finland	CO_2+T	Matala et al.2005
Total Yield	plus	0	18	0	18	100'	FINNFOR	Boreal	Finland	CO_2+T	Matala et al.2006
Biomass (wood)	plus	0	4	0	4	1990-2100'	RipFor	Boreal	Estonia	CO_2+P+T	Nilson et al. 1999
Biomass (wood)	plus	0	3	0	3	100'	ForSVA	Temperate	Canada	P+T	Oja & Arp 1996
Volume	plus/minus/null	6	17	1	24	10*	CABALA	Temperate	Australia	CO_2+P+T	Pinkard et al. 2010
Biomass (above+belowground)	plus	0	9	0	9	100'	Century 4.0	Boreal	Canada	P+T	Price et al. 1999
Biomass (above+belowground)	minus	6	0	0	6	6*	BALANCE	Temperate	Germany	P, P+T	Rötzer et al. 2009
Harvested Wood	plus	0	4	0	4	145'	EFIMOD-2	Boreal	Canada	P+T	Shaw et al. 2006
accumulated NEP	plus/minus	28	12	0	40	2036-2066'	CenW 3.1	Mediterranean	Australia	CO_2, P, T, CO_2+N+P+T	Simioni et al. 2009
Total Mass (stem)	plus	0	2	0	2	100'	FINNFOR	Boreal	Finland	T, CO_2+T	Väisänen et al. 1994
Overall pools											
Total		57	246	2	305						
Overall											
Total		225	964	20	1209						

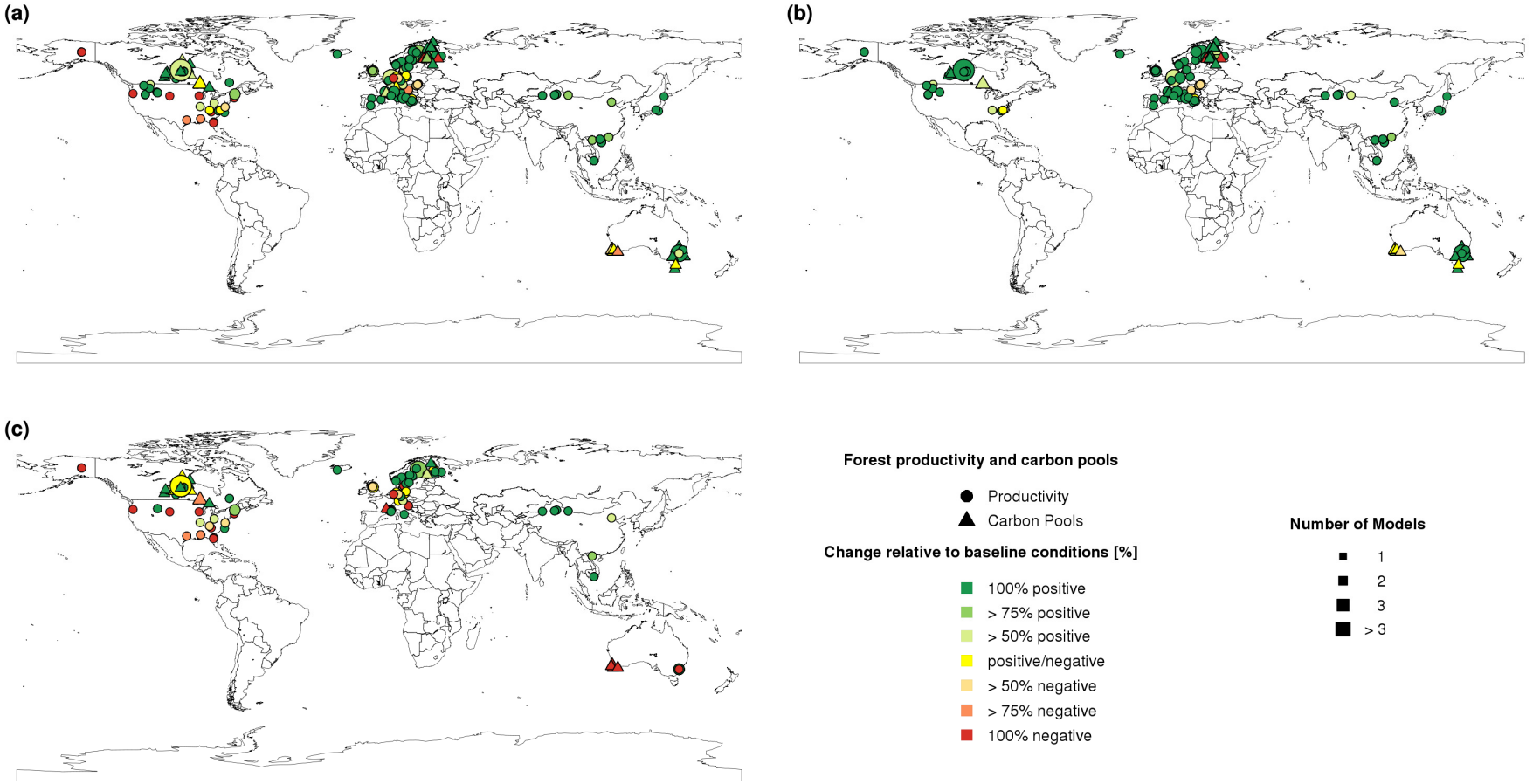

Fig. 2-2 Qualitative future changes in forest productivity (circles) and carbon pools (triangles) under environmental change for (a) all studies, (b) those studies considering climate change and increasing CO_2 in conjunction and (c) those studies considering only climate change. The color scheme indicates the proportion of simulations at each stand resulting in positive or negative changes of forest productivity and carbon pools under environmental change, while the size of the points indicates the number of models applied (small = 1 model, medium = 2 models, large = 3 models, very large > 3 models). Six simulations have been excluded from (b) and (c) since they do not include climate change and/or CO_2 at all (see text for further explanations).

2.3.2 Quantitative analysis of simulations driven by transient change in climate and CO_2

Since climate and CO_2 are gradually changing and not stepwise, this subset of the dataset only included those simulations in which climate change, CO_2, and their combination had been changed in a transient way. Furthermore, six simulations from two studies that only provided a qualitative assessment of changes were excluded to focus on quantifiable changes in response variables. This selection resulted in 525 simulations from 23 models and 40 different studies.

The transient simulations show distinct changes in forest productivity and carbon pools under environmental change in different biomes (Fig. 2-3). Whereas the response in boreal forests is mostly positive, it is less clear in temperate and especially Mediterranean forests although the median is always positive. While for boreal forests the change in forest productivity and carbon pools relative to baseline conditions varies from -11 to 75% (with one outlier at 148%), the change varies from -45 to 67% (with two larger outliers) and from -52 to 77% (with several larger outliers) in temperate and Mediterranean forests respectively.

To synthesize the effects of climate change, CO_2 and their combination on the changes in biomass and productivity relative to baseline conditions, we pooled the transient simulations in these three categories (Fig. 2-4). The effects of a changing climate investigated separately from increasing CO_2 led to both positive and negative changes in forest productivity and carbon pools relative to baseline conditions ranging from -20 to 33% including several negative and positive outliers. In contrast, the simulations including only the effects of increasing CO_2 always resulted in positive changes (from 2 to 58% with one larger outlier). When climate change effects and increasing CO_2 where simulated in combination, most of the simulations showed positive changes in forest productivity and carbon pools relative to baseline conditions (with several outliers showing very strong positive changes).

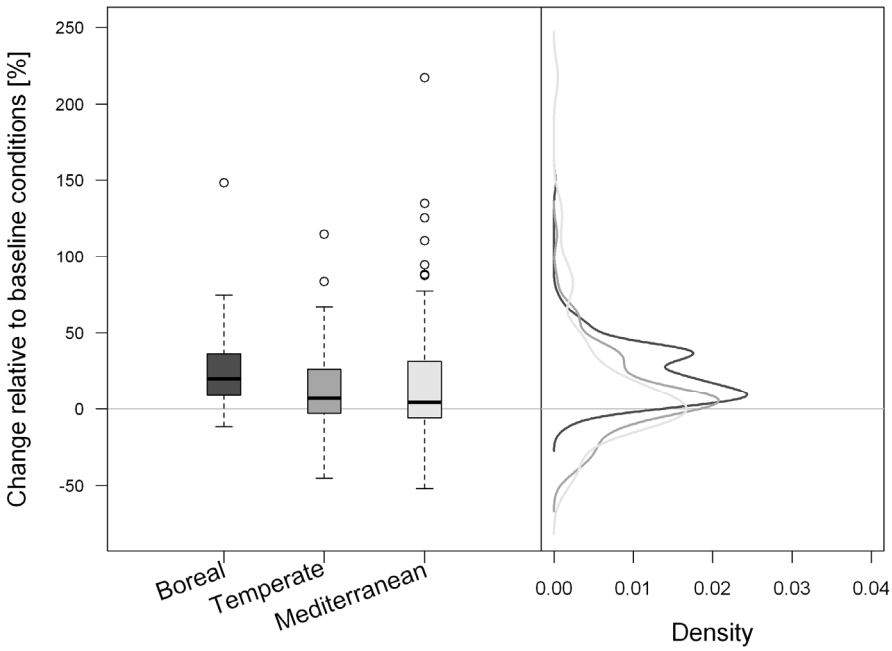

Fig. 2-3 Changes in forest productivity and carbon pools under different environmental change scenarios in three biomes (boreal: simulations = 305, models = 12, studies = 26; temperate: simulations = 142, models = 10, studies = 12; Mediterranean: simulations = 78, models = 4, studies = 4). The grey line indicates no change compared to the baseline scenario. The boxplots show the following information: thick line= median, bottom and top of the box = 25th and 75th percentiles, whiskers = maximum value or 1.5 times the interquartile range of the data depending on which is smaller. Points = outliers larger than 1.5 times interquartile range. The density curves represent kernel density estimates of the changes in forest productivity and carbon pools (using Gaussian kernels and a smoothing bandwidth scaled with the standard deviation of the kernel).

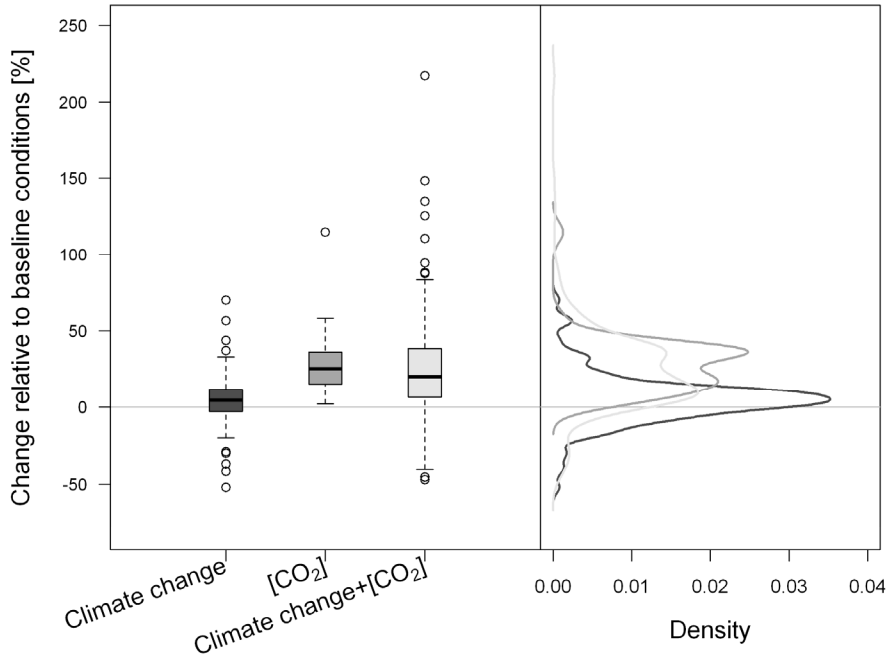

Fig. 2-4 Changes in forest productivity and carbon pools under different drivers of global change. Climate change = changing temperature and precipitation, CO_2 = increasing atmospheric CO_2, Climate change+CO_2 = combination of Climate change and CO_2. (Climate change: simulations = 137, models = 15, studies = 19; CO_2: simulations = 48, models = 11, studies = 12; Climate change+CO_2: simulations = 340, models = 17, studies = 31). The grey line, boxplots and probability density curves are as in Fig. 2-3.

2.3.3 Quantitative analysis of simulations combining climate change and CO_2-effects driven by transient change

The simulations in the database that are driven by scenarios of climate change combined with elevated CO_2 represent the most realistic combination of drivers of environmental change compared to simulations were only one factor is changing. Therefore, we considered only these simulations to assess changes in forest productivity and carbon pools under different decadal warming rates. This selection resulted in 338 simulations from 17 models and 31 different studies. The median change relative to baseline conditions was always positive (and significantly different from zero) and peaked between 0.4 and 0.5K of decadal warming rate (for more information see Fig. 2-5). In these two classes also most of the highest positive outliers occurred while the most negative changes were located in the classes 0.2-0.3K and larger than 0.6K warming per decade.

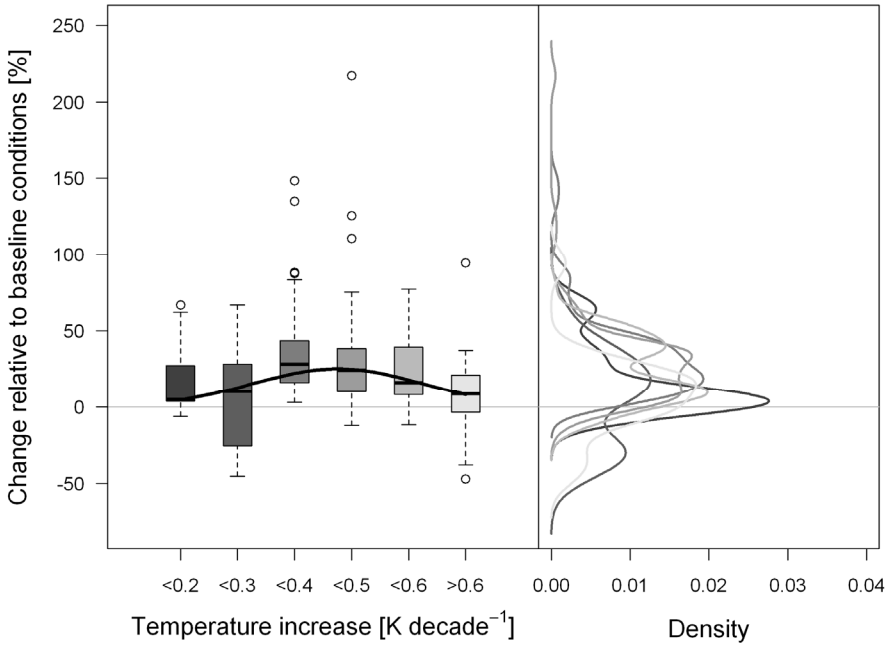

Fig. 2-5 Changes in forest productivity and carbon pools under different decadal warming rates. <0.2 = temperature change below 0.2K per decade; <0.3 = temperature change below 0.3K per decade; <0.4 = temperature change below 0.4K per decade; <0.5 = temperature change below 0.5K per decade; <0.6 = temperature change below 0.6K per decade; >0.6 = temperature change above 0.6K per decade). (<0.2: simulations = 15, models = 6, studies = 5; <0.3: simulations = 44, models = 7, studies = 9; <0.4: simulations = 74, models = 8, studies = 9; <0.5: simulations = 99, models = 8, studies = 14; <0.6: simulations = 80, models = 5, studies = 10; >0.6: simulations = 26, models = 5, studies = 5). The thick black line represents a back-transformed model fitted through the log-transformed medians of each temperature class increase. The log-transformed model has the form: log(Y)=a*T2+bT+c, where Y is the change in productivity and biomass relative to baseline conditions, T is the temperature increase class and a, b and c are parameters with the values a= -22.1753 (Std. Error = 3.3281; t-value = -6.663; P<0.01), 21.0791 (Std. Error = 3.0345; t-value = 6.947; P<0.01) and -1.7852 (Std. Error = 0.6225; not significant) respectively. The adjusted R2 of the model equals 0.90 and the model is significant at p<0.05 (F-value = 24.86). The grey line, boxplots and probability density curves are as in Fig. 2-3.

2.4 Discussion

2.4.1 Literature search, data compilation and analysis

We present a thorough and systematic synthesis of the published, peer-reviewed literature on stand-scale process-based modeling of the impacts of environmental change on forest productivity and carbon pools. As with any other literature analysis, the results depend on the simulations we found and missing references may influence them. However, the Web of Science is considered one of the most appropriate scientific literature search tools (Jasco 2005). Furthermore, by using a wide range of search terms to account for the diversity of drivers and models and by continuously comparing the papers found in the search with those cited in them, we can exclude that a large number of papers escaped our attention. We only had to update our database once with a paper that fitted the search criteria but was not detected by the literature search. This corroborates the generality and validity of our literature search and to our knowledge this study represents the most comprehensive compilation of published studies of simulated changes in forest productivity and carbon pools under environmental change.

Our results are also sensitive to the selection of which model types to include. We broadly followed Medlyn et al. (2011)'s checklist for evaluating model studies which contains a very useful classification of model types. However, there will always be some subjectivity in model classification and we acknowledge that using another classification might have influenced our selection to a certain degree.

Another important assumption of this study is the choice of only considering relative rather than absolute changes of the response variables. We use the change in forest productivity and carbon pools relative to baseline conditions as response variable since this is most commonly reported. Moreover, models may not predict the absolute values of the response variables very accurately making relative changes more suitable for this study. Furthermore, considering the relative change in response variables supports our second synthesis method, namely pooling the response variables. It is evident, that the response variables pooled in this study describe different characteristics of a forest stand. For example, higher photosynthesis does not necessarily translate into higher tree growth (Berninger et al. 2004) or relationships between forest productivity and biomass may not be always linear (e.g. Keeling & Phillips 2007 but see Ciais et al. 2008). However, since we analyze the relative changes in the response variables to assess the effect of different driving variables pooling them seems a valid approach.

Publication bias might be another potential limitation of our study. The number of publications reporting no change of response variables is very low in our dataset .This may be caused by a publication bias towards studies showing clear positive or negative effects of environmental change on forest productivity and carbon pools. There are two ways to take publication bias into account (Moller & Jennions 2001): The direct method is to go to the 'source population', which in our case would be all modeling studies on future forest productivity and carbon pools under environmental change that have been carried out. Besides practically being impossible, this would mean that we had to include many other studies from unpublished/grey literature sources which contradicts our focus on published and peer-reviewed studies. If we consider published and peer-reviewed articles as the source population however, our analysis is quite close to it. The indirect methods such as funnel graphs are not applicable because of the deterministic nature of the models. Thus, we can not rule out the possibility of a publication bias towards studies showing changes of forest productivity and carbon pools under environmental change. However, there are no strong reasons to expect a publication bias towards either positive or negative changes. Furthermore, most of the studies feature simulations of different species, different sites, and/or different scenarios and should thus report results of all directions and magnitudes. Actually there are only five papers included in our dataset that only consider one simulation (Table 2-1).

2.4.2 Uncertainties

One important aspect of this study was to display uncertainty ranges of the projected changes in forest productivity and carbon pools across a wide range of conditions. Therefore, we focused on synthesizing results from a broad array of studies and included different locations, species, stand ages and even management types,. By showing the full range of the results and by indicating the number of models, simulations and studies we highlight how reliable the projected changes are across different model structures. Hence, our analysis accounts for uncertainties in model structure, since we present changes that transcend the methodological variability of the models. Since we are not evaluating the models regarding their quality or ability to precisely describe relevant processes, we assume that the models are equally good and independent. This is a common but not unchallenged assumption in model comparison studies (Tebaldi & Knutti 2007; Medlyn et al. 2011). In reality, the models are not fully independent since they share submodels for specific processes such as the description of photosynthesis. Additionally, some models are more

widely used than others, have more published applications or more simulations per application so that they may be overrepresented in our dataset. Weighting the models may help quantify uncertainties but would require more synchronized model comparisons (e.g. van Oijen et al. 2013) which are beyond the scope of this synthesis. We also did not analyze the way how different processes are formulated in the models which would explain the results of each individual model, because this has been done in an exemplary way elsewhere (Medlyn et al. 2011). Our objective was to synthesize the model results rather than the processes that lead to them. Thus, it is not possible to designate the most important processes in the models at the level of process description. In the following sections we discuss whether the overall response we found is consistent with the current ecological understanding of productivity changes and their causes from experimental and observational studies.

2.4.3 Qualitative analysis of all studies found in the literature search

The analysis of all studies found in the literature search revealed several important biases of current efforts to model effects of environmental change on forest productivity and carbon pools at the stand-scale. Firstly, there is a clear regional focus on temperate and boreal forests in North America and Europe. We did not find any study in South-America and Africa at all, although there is strong and partly conflicting evidence that forest productivity is changing in these regions (e.g. Laurance et al. 2004; Lewis et al. 2004 but Feeley et al. 2007; Silva & Madhur 2012). Secondly, the selection of forest systems which are described by detailed stand-scale process-based models is restricted to mostly mono-specific forests and tree species that are relevant for forestry. Systems and species which are more important for other ecosystem functions and services are only rarely addressed. This bias in plot and system selection can be partly explained by the large amount of physiological data that is necessary to drive PBMs and which is usually only available from long-term and intensive monitoring plots. Thirdly, our assessment of the different environmental drivers being covered reveals a focus on climate change and increasing CO_2. Only few studies looked at other drivers such as nitrogen or ozone (especially not in isolation) although these have been identified as important drivers in the past (Felzer et al. 2004, Kahle et al. 2008). This bias may be less important since the effect of nitrogen is considered to be comparably low in the future (Reay et al. 2008). Nonetheless, it would still be important to assess and test this finding with forest models.

Having this in mind, our qualitative analysis clearly shows that most of the responses of forest productivity and carbon pools to the different environmental change drivers and their combinations are positive especially if climate change and increasing CO_2 are combined. If only climate change is considered, 35% of the simulations show negative responses. This highlights the importance of the effects of increasing CO_2 on plant productivity by enhancing photosynthesis and water use (Körner 2006; Leuzinger & Körner 2007). There is increasing observational and experimental evidence that the strength and persistence of the CO_2-effect may however depend largely on nutrient availability and soil fertility, physiological acclimation, time, age and droughts (Körner et al. 2005; Körner 2006; Norby et al. 2010; Penuelas et al. 2011) and whether studied at the leaf, canopy or landscape scale (Field et al. 1995). These effects are not fully accounted for in the models (see also Fontes et al. 2010).

2.4.4 Qualitative analysis of simulations driven by transient change

This part of the analysis focused on the relative changes in forest productivity and carbon pools in different biomes and on the influence of climate change, increasing CO_2 and their combination as major drivers in the PBMs. Fig. 2-4 shows that climate change may decrease or increase forest productivity and carbon pools. In contrast, increasing CO_2 has always and the combination of climate change and increasing CO_2 most of the time positive effects. It is also evident that despite these general trends, there is a huge variation in the magnitude of the change which maybe an artifact of the different model assumptions and processes, the initial conditions and the environmental changes imposed. These results are consistent with model comparisons from global-scale model comparisons (Cramer et al. 2001).

The positive response we find in model simulations for boreal forests is in line with past ground-based and satellite measurements (Kauppi et al. 1992; Spiecker et al. 1996; Myneni et al. 1997; Nemani et al. 2003; Boisvenue & Running 2006; Zhao & Running 2010; Silva & Madhur 2012) and the current understanding that temperature is a strongly limiting factor of forest productivity. Increasing temperatures and a concomitant lengthening of the growing season as well as increasing nutrient availability (through decomposition and mineralization) exert a strong positive effect on forest productivity and carbon pools (Jarvis & Linder 2000; Lucht et al. 2002; Way & Oren 2010) as long as water availability is not limiting (e.g. as in Ge et al. 2010) and enough light is available. These mechanisms are also relevant in temperate forests but there is evidence that a broader variety of environmental conditions controls productivity in these systems (e.g. Dittmar et al. 2003; Bontemps et al.

2009; Charru et al. 2010). This variability and increased vulnerability to drier and warmer conditions is reflected by the larger amount of negative changes in forest productivity and carbon pools relative to baseline conditions in our dataset. In Mediterranean conditions, drier and warmer conditions in recent decades have strongly influenced forest conditions and growth (Sarris et al. 2010; Carnicer et al. 2011; Vayreda et al. 2012). While this sensitivity is supported by the simulations yielding negative changes in forest productivity and carbon pools in our dataset, a larger part of the simulations show positive changes which contradicts common expectations of growth decline under climate change in the Mediterranean. This finding is strongly related to the importance of CO_2 and the climate change scenarios used in the simulations. Under water shortages the effects of elevated CO_2 on stomatal conductance leading to enhanced water-use-efficiency (Kirschbaum 2000; Keenan et al. 2011) are most pronounced. However, recent carbon isotope tree ring studies show that this effect has not been translated into increased tree growth but may have been overridden by drought, warming, nitrogen limitation or physiological adjustments (Penuelas et al. 2008; Penuelas et al. 2011; Silva & Madhur 2012). Interestingly, those simulations in our dataset in the Mediterranean that do not include effects of elevated CO_2 (i.e. Kramer et al. 2000; Simioni et al. 2009) project exclusively negative changes in forest productivity and carbon pools relative to baseline conditions.

In summary, our results show a mostly positive response of boreal forests to climate change and increasing CO_2 which is consistent with expectations from observations, experiments, larger scale modeling efforts and theory while temperate and especially Mediterranean forests show more ambivalent responses as a result of increasing CO_2. This highlights the regional differentiation of climate change effects on forest productivity and carbon pools (increasing if temperature-limited and decreasing if water-limited) in contrast to a general positive effect of increasing CO_2. This regional differentiation is consistent with recent stand-scale carbon isotope studies (Silva & Madhur 2012).

2.4.5 Qualitative analysis of simulations combining climate change and CO_2-effects driven by transient change

Despite the incomplete understanding of the effects of CO_2 on forest productivity outlined in earlier sections, we still consider that the simulations that are driven by a combination of climate change and increasing CO_2 represent the most realistic combination of drivers of environmental change compared to simulations were only one factor is changing. For these simulations, we find that the response of forest productivity and carbon pools to

environmental change follows an optimum function (Fig. 2-5). The simulated forests respond positively to climate change and increasing CO_2 until a decadal warming rate of 0.4-0.5K. Thereafter, at higher decadal warming rates, the response turns increasingly negative. This result is consistent through the different quartiles of the distributions of each class of temperature increase with a notable exception of one study (Hlásny et al. 2011) which contains all negative simulations of the 0.3K decadal warming rate class. This threshold decadal warming rate of 0.4-0.5K represents a rather high limit of temperature increase considering that the rate of global warming over the period 1956-2005 has been around 0.13K per decade and that the projected ranges until 2099 range between 0.18 to 0.64K per decade (IPCC 2007a). However, the range of temperature increase we find is within the range of projections. More importantly it is very sensitive to our current understanding of the positive effects of increasing CO_2 on forest productivity whose persistence over time and space is uncertain (Körner 2006; Norby et al. 2010). Furthermore, our database does not consider the impacts of altered disturbances regimes and extreme events such as fire, insects or storms on forest productivity and carbon pools (e.g. Kurz et al. 2008) which may limit or reverse positive effects of climate change already at lower degrees of warming. It is also unclear to which degree PBMs include higher order interactions such as higher growth rates that lead to decreased longevity (Bugmann & Bigler 2011; di Filippo et al. 2012) or extreme physiological events (such as drought-induced mortality (Reyer et al. 2013)). The latter are more important predictors of forest productivity and carbon pools (e.g. Zhao & Running 2010) than mean climate (Stegen et al. 2011). In summary, the positive physiological response (i.e. without considering altered disturbance regimes) of forest productivity and carbon pools to climate change and increasing CO_2 culminates at a decadal warming rate of 0.4-0.5K and declines thereafter.

2.4.6 Synthesis and implications for modeling

This paper shows that stand-scale process-based models simulate a broad variety of responses of forest productivity and carbon pools to climate change and elevated CO_2. The models agree on mostly positive responses in boreal and more ambivalent responses in temperate and Mediterranean forests depending on the importance of individual environmental variables. However, there are large uncertainties regarding the absolute value of these responses as a result of different model structures, site conditions, magnitudes of environmental change and the long-term persistence of CO_2-effects. The synthesis of published studies may have limitations and represents a high variability due to

different data sets, time frames, assumptions etc. but the overall responses transcend this variability. It is noteworthy that these studies cover the physiological response to environmental change, but that at larger spatial scales the effects of disturbances and management shifts, shape the state of forest ecosystems. Our work serves to inform regional studies which strive to integrate changes in forest productivity and carbon pools with disturbances or other socioeconomic drivers to, for example, develop adaptive management strategies. Furthermore, this paper provides a synthesis of published model-based changes in forest productivity and carbon pools with which the results of further studies can be compared. Our results can be refined by more structured model intercomparisons with improved stand-scale PBMs.

Our synthesis also finds that past modeling efforts have largely focused on species important for forestry, particular biomes and prominent environmental variables. This is partly due to constraints in data availability to parameterize complex models. Nevertheless, further studies may exploit newly available datasets as well as data integration and uncertainty quantification techniques to cover a larger array of forest stands, species, biomes, environmental drivers and thus different ecosystem services and functions and corresponding challenges. Moreover, further studies could make better use of the strengths that differentiate modeling approaches from observational and experimental studies: To simulate the effects of a multitude of single environmental drivers and their combinations in full factorial designs in a transient way.

2.5 Acknowledgements

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3 Projecting regional changes in forest net primary productivity in Europe driven by climate change and carbon dioxide concentration[2]

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Abstract

Projecting changes in forest productivity in Europe is crucial information for adapting forest management to changing environmental conditions. The objective of this paper is to project forest productivity changes under different climate change scenarios at a large number of sites in Europe with a stand-scale process-based model. We applied the process-based forest growth model 4C at 132 typical forest sites of Europe's five most important tree species in ten environmental zones using climate change scenarios from three different climate models and two different assumptions about CO_2-effects on productivity. This paper shows that future forest productivity will be affected by climate change and that these effects depend strongly on the climate scenario used and the persistence of CO_2-effects. We find that productivity increases in Northern Europe, increases or decreases in Central Europe and decreases in Southern Europe. It is important to note that we consider the physiological response to climate change excluding disturbances or management. Different climate change scenarios and model structural uncertainties lead to uncertain projections of future forest productivity. These uncertainties need to be integrated into forest management planning and adaptation of forest management to climate change using adaptive management frameworks.

Keywords: 4C (FORESEE), Climate Change, CO_2, Europe, Process-based modeling, Net Primary Productivity

3.1 Introduction

Productivity is a key ecological variable for forest management and also highly relevant to understand carbon cycling in forest ecosystems. Ground-based measurements and satellite data have indicated shifts in forest productivity in past decades (e.g. Kauppi et al. 1992; Spiecker et al. 1996; Myneni et al. 1997; Nemani et al. 2003; Boisvenue & Running 2006; Kahle et al. 2008). In Europe, climate change, increasing atmospheric CO_2 concentrations and nitrogen deposition but also land use changes and recovery from past management combined with novel management practices have been highlighted as possible causes (Spiecker et al. 1996; Boisvenue & Running 2006; de Vries et al. 2006; Solberg et al. 2009).

Forest management has to adapt to changing environmental conditions to ensure the functions and services forest ecosystems provide to society. Therefore, knowing if, where and with which magnitude past productivity changes will continue or reverse is crucial. Process-based models (PBMs) describe changes in responses to environmental variables based on plant physiology and are thus suitable tools to simulate climate change impacts on forests and to assess adaptive forest management strategies (Fontes et al. 2010; Chmura et al. 2011). Stand-level PBMs simulate processes for typical forest stands and provide detailed physiological and structural output. They require detailed input data for stand and site initialization (Fontes et al. 2010) and for species-specific parameters, which are derived from physiological measurements (Landsberg 2003). Thus, they represent local physiological-based responses to environmental change and only seldom integrate processes that occur at the landscape scale such as disturbances (Seidl et al. 2011).

Even without considering disturbances, projections of future forest productivity changes are associated with several types of uncertainties. These uncertainties result from uncertainties in climate change scenarios, model parameters and model structure. Climate change scenario uncertainty is a combination of uncertainties in projections of future greenhouse gas emissions (and the resulting climate change) and the different climate change trajectories simulated by different climate models using the same forcing. In the case of forest modeling this is essentially a model input uncertainty. An example for model structural uncertainty is the increasing evidence that effects of carbon dioxide (CO_2) which are commonly integrated into PBMs are rather a transient phenomenon at the tree and forest stand level. After an initial increase, productivity becomes limited by other factors such as nutrient availability and plants acclimate to elevated CO_2 (Körner et al. 2005; Norby et al. 2010). However, there is no full explanation of these effects yet and model formulations accounting for these feedbacks are lacking.

The objective of this paper is to project forest productivity changes at a large number of sites in Europe with one single stand-scale PBM. Furthermore, to account for climate change scenario uncertainty, we rely on several climate change scenarios from different regional climate models. We use international and newly available databases (e.g. ICP Forests Network, EUROFLUX, European Soil Database) that are crucial for studies simulating forest productivity under changing environmental conditions (Bugmann et al. 2010). This approach allows for an identification of expected hotspots of changes and of uncertainty in forest productivity for the five most important European tree species (Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L. Karst.), European beech (*Fagus sylvatica* L.) and Sessile and Pedunculate oak (*Quercus petraea* Liebl. and *Quercus robur* L.) in ten environmental zones in Europe as defined by Metzger et al. (2005).

It is important to note, that our analysis does not cover Mediterranean tree species but is restricted to boreal and temperate species that occur in the Mediterranean in higher altitudes. Furthermore we only describe the physiological responses to global change and although considering managed forests, we do not include management or disturbances.

3.2 Material and methods

3.2.1 The model 4C

The model 4C ('FORESEE' - Forest Ecosystems in a Changing Environment) has been developed to describe long-term forest behavior under changing environmental conditions (Bugmann et al. 1997; Lasch et al. 2005). It describes processes on tree- and stand-level based on findings from eco-physiological experiments, long term observations and physiological modeling. The model includes descriptions of tree species composition, forest structure, leaf area index as well as ecosystem carbon and water balances. Establishment, growth and mortality of tree cohorts are explicitly modeled on a patch on which horizontal homogeneity is assumed. The soil sub-model describes temperature, and water, carbon and nitrogen dynamics in different soil layers. 4C requires daily meteorological variables as well as a soil and a forest stand description.

Currently the model is parameterized for 11 tree species, particularly the five most abundant tree species of Central Europe (European beech, Norway spruce, Scots pine, Pedunculate and Sessile oak). A more detailed description of 4C can be found in the Appendix to chapter 3. In the framework of this study, the different model processes have been validated at nine

stands across Europe with detailed measurements from different sources. For a detailed description of the validation concept, data and results see the Appendix to chapter 3.

3.2.2 Data

Stand data

The stand data used to initialize 4C stems from several sources. The largest part consists of individual tree data derived from the Level-II plots of the 'Pan-European Programme for Intensive and Continuous Monitoring of Forest Ecosystems' database (hereafter referred to as Level-II database) which represents typical forest stands in most European countries (de Vries et al. 2003) and is unique in spatial coverage. Additional sites that were added especially for model validation purposes were taken from the EUROFLUX network (Cermak et al. 1998; Schulze 2000; FW Badeck, A. Granier Pers. Comm., 2005) and the NORDFLUX project (P. Kolari, Pers. Comm. January 2011). We focused on the five most important tree species in Europe, namely Scots pine, Norway spruce, European beech and Sessile and Pedunculate oak. The latter two species were not distinguished in this study. Within the Level-II database we selected a large number of sites for which sufficient data was available to initialize 4C to cover most of Europe's growing conditions (for further information on site selection see the Fig. 9-1). The final number of sites was 132 (Table 9-1) and covers the age, soil and geographic distribution as well as the management history of European forests as far as data was available and as far as the Level-II database is considered to represent typical forests. Our selection does not represent the area or importance of a species in the individual countries. The 132 sites fell into 10 environmental zones as defined by Metzger et al. (2005; Table 3-1).

Table 3-1 Number of stands per tree species in each environmental zone (after Metzger et al. 2005).

Environmental zone	*Fagus sylvatica*	*Picea abies*	*Pinus sylvestris*	*Quercus robur/petraea*	Total
Alpine North (ALN)	-	4	2	-	6
Boreal (BOR)	-	6	12	-	18
Nemoral (NEM)	3	8	3	1	15
Atlantic North (ATN)	5	3	2	-	10
Alpine South (ALS)	1	4	1	-	6
Continental (CON)	15	14	14	4	47
Atlantic Central (ATC)	9	-	5	4	18
Pannonian (PAN)	-	1	-	1	2
Lusitanian (LUS)	-	-	1	2	3
Mediterranean Mountains (MDM)	4	-	3	-	7
Total	37	40	43	12	132

Climate data, climate change scenarios and CO_2

Our simulations were driven by daily climate time series of temperature, precipitation, relative humidity, global radiation, air pressure and wind speed for the past and the future. We used data of three different Regional Climate Models (RCM) driven by three different General Circulation Models (GCM) in the following RCM/GCM combinations: CCLM/ECHAM5, HadRM3/HadCM3 and HIRHAM3/Arpège. The data of the latter two RCM/GCM combinations has been taken from the ENSEMBLES project (van der Linen & Mitchell 2009) while the CCLM/ECHAM5 data is from Lautenschläger et al. (2009a-f). For each RCM/GCM combination one realization for the period 1971-2000 was available for the past climate and one for the period 2001-2090 for the future climate according to the SRES CO_2-emission scenario A1B (Nakicenovic et al. 2000). For CCLM we also used a second realization for the period 1971-2000 and a corresponding second realization of the A1B run as well as two realizations of the SRES CO_2-emission scenario B1 (Nakicenovic et al. 2000) also for the period 2001-2090. This resulted in four realizations of three RCM/GCM combinations for A1B and two realizations of one RCM/GCM combination for the B1. For more information on the realizations see the Appendix to chapter 3.

Since the RCMs do not always fit observed data (e.g. Hollweg et al. (2008) noted that generally summers are too cold and precipitation is too high in the CCLM runs), we corrected mean temperature and precipitation with data from a measured dataset (CRUPIK) for absolute and relative model bias respectively (Appendix to chapter 3). The mean temperature of this dataset is a version of the CRU data set (New et al. 1999; New et al. 2000; Mitchell & Jones 2005) corrected and homogenized at PIK (Österle et al. 2003). The precipitation dataset is a version of the Global Precipitation Climatology Centre (Fuchs 2008; Rudolf & Scheider 2005; Rudolf et al. 2010; Scheider et al. 2008) corrected and homogenized at PIK (H. Österle Pers. Comm. 2010).

This climate data was downscaled to the location of the 132 plots. To account for altitudinal dependencies of the climatic variables we used information from a digital elevation model of the Global Land Cover Facility (USGS 2004) and external-drift-Kriging (Deutsch & Journel 1992). Wind speed did not show any height dependency and was interpolated using ordinary-Kriging (Deutsch & Journel 1992). After the interpolation, the data was checked for plausibility since the bias-correction as well as the interpolation can introduce physically implausible values of daily weather. For example, the relative correction of precipitation can lead to very high daily precipitation sums which were then reduced to physically plausible values.

Once the climate data was bias-corrected and downscaled, we generated a set of climate change scenarios for each site: Each of the six realizations was dissected into three time slices of future time periods (P1=2001-2030, P2=2031-2060, P3=2061-2090) yielding 18 different climate change pathways. Each of these was then combined with an assumption on future CO_2 – either constant at 350ppm or increasing corresponding to the CO_2-emission scenarios A1B or B1 – to represent two diverging hypotheses about the persistence of CO_2-effects. Constant CO_2 represents the lower margin (i.e. current CO_2-effects), whereas increasing CO_2 represents the upper margin (i.e. persisting CO_2-effects) of CO_2-effects on NPP in our analysis. The time slices represent physically realistic combinations of temperature and precipitation and two different assumptions about CO_2 and are treated as independent climate change scenarios. By this method we obtained six (realizations) times three (time slices) times two (CO_2 assumptions) equals 36 climate change scenarios. Each of these was linked to its respective realization of the past climate (1971-2000) including either constant CO_2 at 350ppm or increasing CO_2 corresponding to the Mauna Loa data (Tans & Keeling 2012) leading to four realizations of past climate times two CO_2 assumptions equals eight baseline scenarios. An aggregated analysis of the climate data for the 10 study regions can be found in Table 3-2.

Table 3-2 Mean annual temperature (T) and mean annual precipitation sum (P) per environmental zone (Metzger et al. 2005, for abbreviations see Table 3-1) and each RCM/GCM combination (CCLM/ECHAM5 (CCLM), HadRM3/HadCM3 (HAD) and HIRHAM3/Arpège (HIR)), CO_2-emission scenario (A1B or B1), realization (R1 or R2) and time slice (Base=1971-2000, P1=2001-2030, P2=2031-2060, P3=2061-2090) considered in this study.

	ALN	BOR	NEM	ATN	ALS	CON	ATC	PAN	LUS	MDM	Constant / Increasing CO_2
						T [°C]					[ppm]
CCLM-R1-Base	0.7	2.9	7.2	9.3	6.9	8.4	10.6	9.8	12.2	9.3	350 / 345
CCLM-A1B-R1-P1	1.0	3.2	7.6	9.7	7.3	8.8	11.0	10.1	12.6	9.9	350 / 405
CCLM-A1B-R1-P2	2.2	4.4	8.6	10.7	8.3	9.8	12.0	11.2	13.7	11.1	350 / 504
CCLM-A1B-R1-P3	3.6	6.0	10.0	12.0	10.0	11.3	13.4	12.9	15.1	13.0	350 / 619
CCLM-B1-R1-P1	1.0	3.2	7.7	9.8	7.4	8.9	11.0	10.3	12.6	9.9	350 / 399
CCLM-B1-R1-P2	2.0	4.2	8.2	10.2	7.8	9.3	11.4	10.6	12.8	10.3	350 / 469
CCLM-B1-R1-P3	2.8	5.1	9.1	11.0	8.9	10.3	12.3	11.7	13.9	11.6	350 / 522
CCLM-R2-Base	0.5	2.6	7.1	9.2	6.9	8.3	10.5	9.7	12.1	9.2	350 / 345
CCLM-A1B-R2-P1	1.4	3.5	7.9	9.8	7.5	9.0	11.0	10.3	12.6	9.8	350 / 405
CCLM-A1B-R2-P2	2.5	4.9	9.1	11.0	8.8	10.2	12.2	11.6	13.6	11.2	350 / 504
CCLM-A1B-R2-P3	3.8	6.0	10.1	12.0	10.0	11.4	13.4	12.8	14.9	12.8	350 / 619
CCLM-B1-R2-P1	1.6	3.8	8.0	10.0	7.6	9.1	11.2	10.4	12.7	10.0	350 / 399
CCLM-B1-R2-P2	2.1	4.3	8.5	10.4	8.1	9.5	11.6	10.8	13.3	10.7	350 / 469
CCLM-B1-R2-P3	2.9	5.1	9.1	11.1	9.0	10.3	12.4	11.8	14.0	11.7	350 / 522
HAD-R1-Base	1.2	2.7	7.1	9.1	6.9	8.3	10.5	9.8	12.3	8.8	350 / 345
HAD-A1B-R1-P1	2.5	4.1	8.4	10.1	7.9	9.4	11.4	10.9	13.1	9.7	350 / 405
HAD-A1B-R1-P2	4.3	6.0	10.0	11.6	9.6	11.1	12.9	12.5	14.6	11.6	350 / 504
HAD-A1B-R1-P3	5.2	7.0	10.9	12.6	10.8	12.1	13.9	13.7	15.6	12.9	350 / 619
HIR-R1-Base	0.8	2.9	7.2	9.2	6.9	8.4	10.6	10.0	12.3	9.1	350 / 345
HIR-A1B-R1-P1	1.5	3.7	7.8	9.6	7.5	8.9	11.1	10.6	12.9	9.8	350 / 405
HIR-A1B-R1-P2	2.6	4.8	8.6	10.5	8.4	9.8	11.9	11.4	14.0	10.9	350 / 504
HIR-A1B-R1-P3	3.8	6.1	9.4	11.1	9.0	10.4	12.5	11.9	14.3	11.6	350 / 619
						P [mm]					
CCLM-R1-Base	871	615	775	807	853	800	821	754	1015	917	
CCLM-A1B-R1-P1	933	641	834	827	862	830	838	815	969	863	
CCLM-A1B-R1-P2	973	662	859	834	849	830	830	773	922	801	
CCLM-A1B-R1-P3	1013	714	897	839	848	819	835	763	893	759	
CCLM-B1-R1-P1	872	638	816	850	900	847	878	818	1012	910	
CCLM-B1-R1-P2	908	664	832	847	889	838	864	805	998	933	
CCLM-B1-R1-P3	987	691	866	833	867	829	829	790	938	813	
CCLM-R2-Base	891	608	762	798	855	798	817	770	983	901	
CCLM-A1B-R2-P1	929	647	797	831	880	829	846	768	995	878	
CCLM-A1B-R2-P2	961	679	847	847	858	821	845	752	962	835	
CCLM-A1B-R2-P3	1028	713	877	836	817	804	815	706	885	749	
CCLM-B1-R2-P1	928	646	797	809	859	804	822	744	991	872	
CCLM-B1-R2-P2	943	674	825	823	856	815	818	743	952	849	
CCLM-B1-R2-P3	975	680	850	854	851	821	826	718	933	811	
HAD-R1-Base	922	634	785	861	922	843	853	805	978	931	
HAD-A1B-R1-P1	983	673	800	856	915	852	860	800	963	932	
HAD-A1B-R1-P2	1055	714	833	841	873	826	801	757	819	814	
HAD-A1B-R1-P3	1054	739	847	816	865	826	790	751	826	788	
HIR-R1-Base	891	629	772	822	868	796	811	757	937	881	
HIR-A1B-R1-P1	949	659	770	847	898	824	837	776	963	883	
HIR-A1B-R1-P2	943	641	760	751	819	780	754	751	868	794	
HIR-A1B-R1-P3	980	651	698	688	753	713	688	665	783	709	

Soil data

We used different sources of soil data for the 132 sites. Since the Level-II database does not provide sufficient soil information to initialize 4C, we linked each Level-II site with the soil information of the European soil database (ESD) (ESBN 2004). This is described in more detail in the Appendix to chapter 3. For Germany the soil data base BÜK 1000 (BGR 2004) was used.

3.2.3 Simulation experiment

To simulate the effects of climate change and changing CO_2, we ran the same 4C initialization at each of the 132 sites for the 8 baseline and the 36 climate change scenarios each lasting for a period of 30 years. The stands were not managed during these 30-year-simulations and soil vegetation was not considered. To display climate change impacts, we analyzed the relative changes (in percent) of mean annual NPP over the simulation period in relation to the mean annual NPP of the baseline simulation. Thus, we ended up with 1056 (132 sites times 8 baseline scenarios) simulation runs for the baseline period and 4752 (36 scenarios times 132 sites) for the future.

3.2.4 Statistical analyses

We used the R software (R Core Development Team 2011) to calculate the density functions of the NPP change and relied on the standard function of R (package *stats*) to compute kernel density estimates. To test if there are differences in the NPP change between the environmental zones and if there are geographically meaningful groups of NPP change we used the Kruskal-Wallis test which is a non-parametric test to compare multiple ranks. We assumed that our model simulations are independent samples to apply the Kruskal-Wallis test. This test was carried out in STATISTICA (StatSoft Inc 2005).

3.3 Results

3.3.1 NPP changes at the European level in the environmental zones

Over all scenarios (i.e. time slices, realizations, CO_2-emission scenarios and RCMs), the changes in NPP are strongly influenced by our assumptions on CO_2 (Table 3-3; Fig. 3-1; Fig. 3-2). With increasing CO_2, the NPP increases in most simulations and in most regions with

few exceptions mainly in the Mediterranean Mountains and Lusitania (Fig. 3-1). The median of the NPP change ranges between 10 to 20% in the different regions (again with the Mediterranean Mountains and Lusitania having slightly lower values). There seems to be a tendency of decreasing NPP change from north to south but the difference in NPP change in between groups is mostly not significant as indicated by the Kruskal-Wallis test (Fig. 3-1). The homogenous probability density functions of the different regions support this result (Fig. 3-1). The variation of the changes in NPP at the stand-level across the different scenarios, time slices and RCMs is quite large (Fig. 3-2). This translates into large variations of NPP change at the regional level and the changes in NPP encountered in individual regions span a range of about 20 to 45% without considering outliers (Fig. 3-1).

Assuming constant CO_2, the changes in NPP are much smaller, span a range of about 15 to 30% without considering outliers (with the exception of MDM, which spans a range of almost 50%) and turn negative for some scenarios in all environmental zones (Fig. 3-1). The median of the NPP change ranges between -5 to 10%. The tendency towards decreasing NPP changes from north to south is somewhat clearer than under increasing CO_2 (Fig. 3-1). The Kruskal-Wallis test indicates stronger regional differentiation and highlights the Atlantic North as distinct group with the highest median NPP change (Fig. 3-1). This is also illustrated by the diverse shapes of the probability density functions of the regions (Fig. 3-1). The variation of the changes in NPP across the different scenarios at the stand-level is mostly lower than in the case of increasing CO_2 (Fig. 3-2). This translates into lower variations in NPP change at the regional level although it is notable that there are many positive and negative outliers (Fig. 3-1).

These regional patterns of higher NPP change and increasing variability under increasing CO_2 are consistent with the results of the individually simulated forest stands over Europe (Fig. 3-2). Fig. 3-2 also shows that with constant CO_2 the changes in NPP are strongly regionally stratified, with increases in Northern, decreases in Southern and Western and ambivalent responses in Central and Eastern Europe.

Over the three future time slices considered, NPP increases from the first to the third time slice in most environmental zones under increasing CO_2 (Table 3-3). Only in few cases in the Mediterranean Mountains and in Lusitania, the NPP is lower in the third time slice compared to the second. Under constant CO_2, the temporal patterns of NPP change are more diverse (Table 3-3). In environmental zones located in higher latitudes and altitudes (ALN, ALS, BOR, NEM), NPP increases from the first to the third time slice of most climate change scenarios. In contrast, NPP decreases from the first to the third time slice of most climate change

scenarios in the southwestern and southeastern environmental zones (LUS, MDM, PAN). In the Atlantic and Continental environmental zones (ATC, ATN, CON), the changes in NPP are less consistent and do not show clear increasing or decreasing trends over the three time slices and across the different emission scenarios and climate models. More information of changes in NPP in the individual time slices, RCM/GCM combinations, realizations and assumptions on CO_2 is presented in Fig. 9-13 to Fig. 9-18. Furthermore, Table 3-3 shows that the effect of the CO_2-emission scenario on NPP change is lower than the choice of the RCM/GCM combination. For example, the NPP change ranges from -0.4 to 7.2% over the CCLM A1B and B1 scenario runs with constant CO_2 in the Boreal environmental zone, while it ranges from -1 to 19% over the A1B scenario runs only but of the three RCMs.

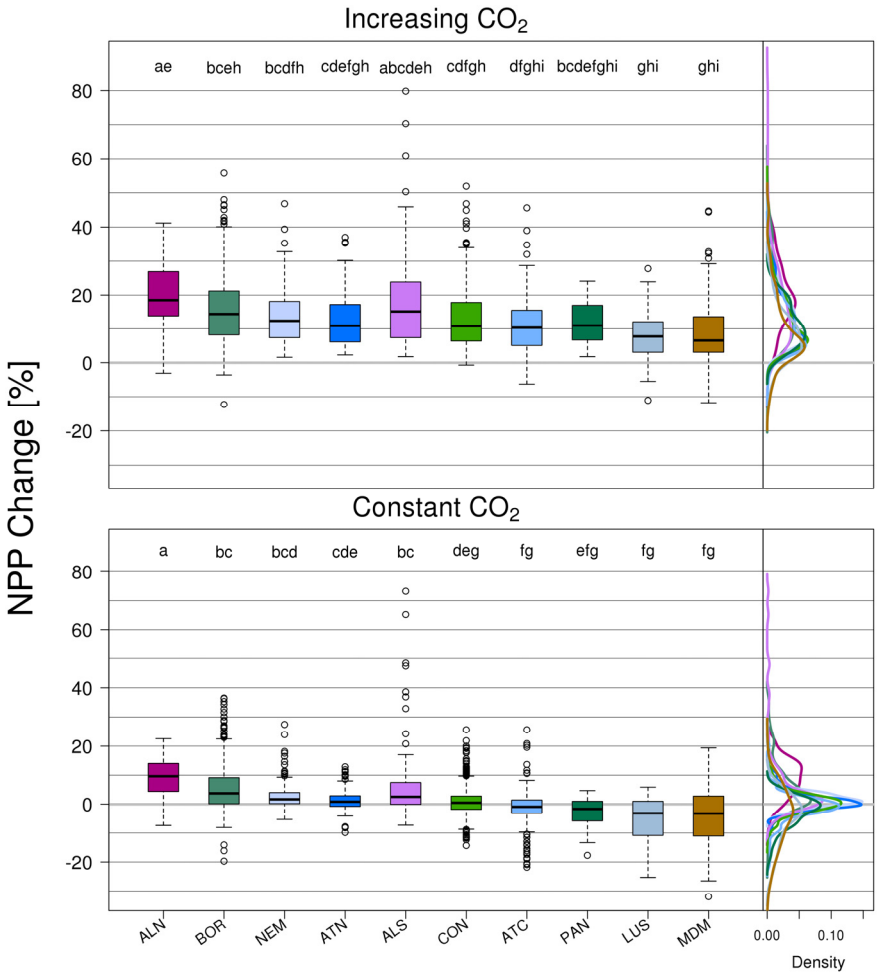

Fig. 3-1 Change in net primary productivity (NPP) in each environmental zone (Metzger et al. 2005, for abbreviations see Table 3-1, color codes as in Fig. 3-2) over all scenarios for simulations with constant and increasing CO_2. Left panels show boxplots, right panels show probability density functions. The vertical line at zero NPP change indicates 'no change' relative to baseline conditions. The lower case letters indicate groups of environmental zones that are significantly different from each other according to the Kruskal-Wallis test. The boxplots show the following information: thick line= median, bottom and top of the box = 25th and 75th percentiles, whiskers = maximum value or 1.5 times the interquartile range of the data depending on which is smaller. Points = outliers larger than 1.5 times interquartile range. The density curves represent kernel density estimates of the changes in forest productivity (using Gaussian kernels and a smoothing bandwidth scaled with the standard deviation of the kernel).

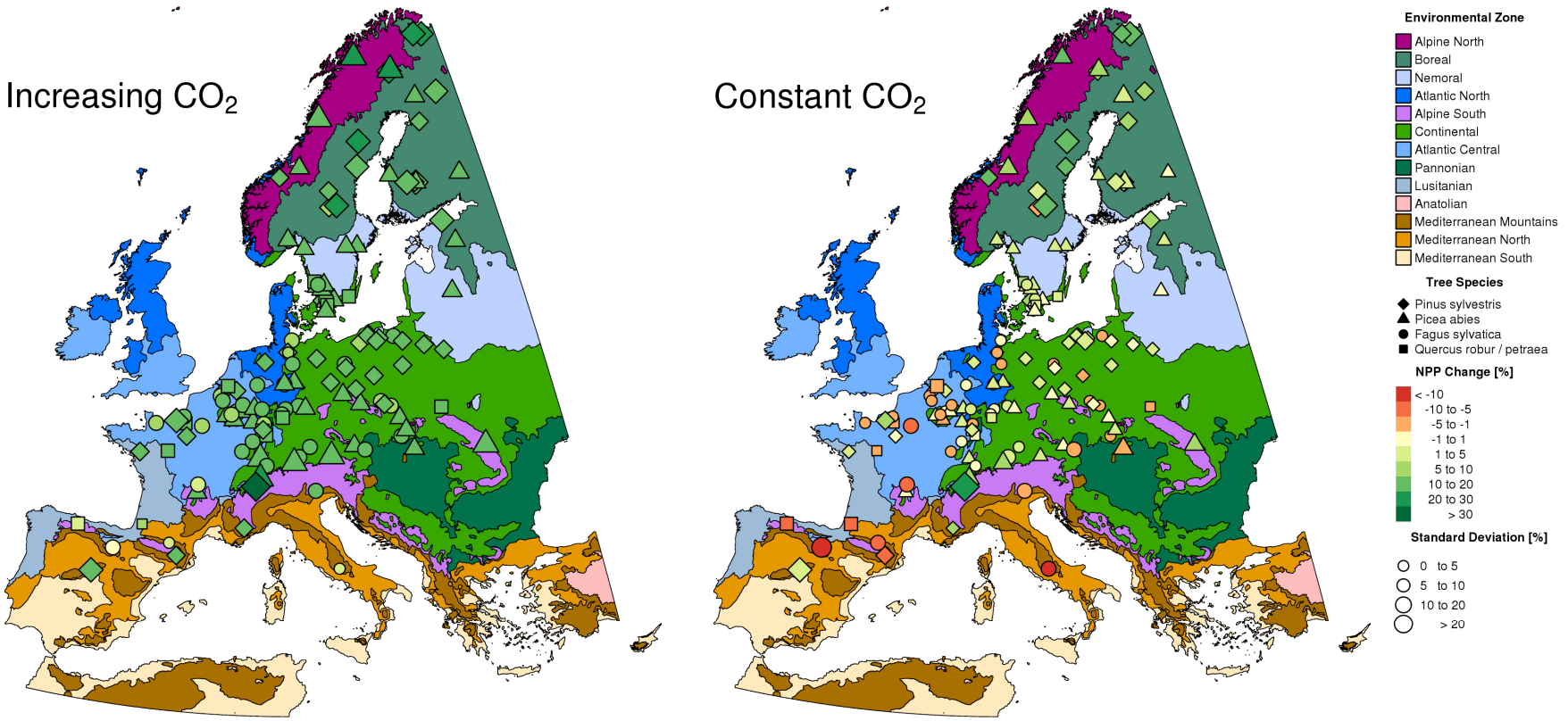

Fig. 3-2 Change in net primary productivity (NPP) for each site averaged over all scenarios for simulations with constant and increasing CO_2. The environmental zones follow the classification of Metzger et al. (2005).

Table 3-3 Changes in net primary productivity (NPP) in % per environmental zone (Metzger et al. 2005, for abbreviations see Table 3-1) and each RCM/GCM combination (CCLM/ECHAM5 (CCLM), HadRM3/HadCM3 (HAD) and HIRHAM3/Arpège (HIR)), CO_2-emission scenario (A1B or B1), realization (R1 or R2) and time slice (P1=2001-2030, P2=2031-2060, P3=2061-2090) considered in this study.

	ALN	BOR	NEM	ATN	ALS	CON	ATC	PAN	LUS	MDM
Constant CO_2										
CCLM-A1B-R1-P1	1.0	0.7	-0.6	-0.2	0.0	-1.8	-1.8	-3.3	-6.6	-6.7
CCLM-A1B-R1-P2	4.3	2.3	1.5	1.1	5.3	-0.7	-0.3	-4.5	-3.8	-4.9
CCLM-A1B-R1-P3	7.0	7.9	3.2	3.7	15.3	1.8	-1.2	-7.5	-11.6	-18.0
CCLM-B1-R1-P1	1.7	3.4	2.5	0.9	0.9	0.5	-1.1	-1.4	-2.3	-1.7
CCLM-B1-R1-P2	7.7	5.3	-0.8	-2.0	0.0	-2.3	-2.9	-3.0	-3.1	-5.0
CCLM-B1-R1-P3	6.2	3.3	3.0	1.9	9.3	1.3	0.8	-0.6	-8.1	-10.5
CCLM-A1B-R2-P1	11.5	4.1	1.7	-0.2	2.3	0.7	0.2	1.6	-0.7	-0.6
CCLM-A1B-R2-P2	13.3	6.6	3.7	2.3	8.8	4.0	2.4	2.8	0.2	1.0
CCLM-A1B-R2-P3	17.7	7.2	3.9	4.3	16.9	4.0	0.2	-3.6	-7.0	-7.6
CCLM-B1-R2-P1	11.4	4.4	3.4	1.7	4.7	2.7	2.0	3.9	-1.6	2.3
CCLM-B1-R2-P2	8.2	-0.4	-0.1	-0.2	4.9	0.3	0.5	1.6	-0.7	-0.3
CCLM-B1-R2-P3	13.6	6.8	1.1	1.5	11.8	3.1	1.2	-2.4	-4.7	-5.4
HAD-A1B-R1-P1	8.9	6.2	2.8	3.2	5.2	0.9	-0.6	-1.2	-0.9	1.7
HAD-A1B-R1-P2	15.8	15.2	7.0	5.4	13.0	2.6	-3.7	-6.6	-12.9	-5.5
HAD-A1B-R1-P3	18.2	19.0	9.0	5.8	14.9	2.9	-4.6	-8.8	-14.5	-6.4
HIR-A1B-R1-P1	-0.6	-1.0	0.3	-0.3	0.7	1.1	-0.9	0.4	2.0	1.5
HIR-A1B-R1-P2	9.6	7.2	0.8	-2.3	2.2	-2.6	-3.8	-4.0	-1.9	-2.8
HIR-A1B-R1-P3	9.4	5.2	1.5	-3.1	-1.3	-5.7	-9.0	-11.8	-11.7	-10.8
Increasing CO_2										
CCLM-A1B-R1-P1	5.7	5.3	4.0	4.6	4.6	3.0	3.4	2.3	-1.2	-1.1
CCLM-A1B-R1-P2	15.1	14.3	12.6	12.8	16.5	11.2	12.6	9.7	10.0	9.6
CCLM-A1B-R1-P3	23.5	25.1	21.2	23.7	35.0	22.9	21.0	17.3	11.7	6.0
CCLM-B1-R1-P1	6.0	7.8	7.2	5.4	5.3	5.1	3.7	4.1	2.5	3.5
CCLM-B1-R1-P2	17.6	14.6	8.1	7.0	8.8	6.9	6.8	8.2	7.3	6.5
CCLM-B1-R1-P3	18.4	16.2	15.6	14.9	22.1	14.8	15.5	16.4	7.9	6.1
CCLM-A1B-R2-P1	16.7	8.9	6.3	4.4	7.0	5.5	5.2	7.6	4.2	5.2
CCLM-A1B-R2-P2	25.4	18.7	15.1	14.0	20.2	16.5	15.0	18.8	13.5	15.6
CCLM-A1B-R2-P3	36.2	24.6	21.8	24.0	36.9	24.6	22.1	22.5	15.4	18.2
CCLM-B1-R2-P1	16.2	8.8	8.0	6.3	9.2	7.5	6.9	9.8	3.4	7.9
CCLM-B1-R2-P2	17.5	8.9	8.6	8.8	13.9	9.7	10.5	13.8	9.8	11.6
CCLM-B1-R2-P3	26.8	20.0	13.4	14.7	25.0	17.1	15.8	14.6	11.4	11.8
HAD-A1B-R1-P1	13.4	10.2	8.1	8.2	9.8	6.1	4.5	4.8	4.6	6.9
HAD-A1B-R1-P2	28.4	27.4	21.3	19.0	26.0	16.8	10.1	8.9	0.6	7.9
HAD-A1B-R1-P3	37.5	36.7	31.7	28.0	36.6	25.9	17.9	15.8	7.6	15.7
HIR-A1B-R1-P1	3.6	3.0	5.2	4.7	5.7	6.5	4.5	6.5	7.8	7.1
HIR-A1B-R1-P2	20.3	17.9	13.5	10.7	15.1	11.2	10.5	10.9	13.3	11.8
HIR-A1B-R1-P3	25.7	22.0	21.6	17.5	18.6	16.1	13.9	12.6	12.4	12.8

3.3.2 NPP changes at the species level

At the species level, the differentiation is also strongest between constant and increasing CO_2 (Fig. 3-3). Generally, the change in NPP ranges from 0 to 40% for coniferous species under increasing CO_2 and from -5 to 20% under constant CO_2 in most environmental zones. For increasing CO_2 exceptions are the Alpine South with much higher and the Mediterranean Mountains with lower values for Scots pine and for constant CO_2 the Boreal, Atlantic Central and Mediterranean Mountains regions for Scots Pine and the Pannonian region for Norway spruce with much lower values as well as the Alpine South with much higher values. For broad-leaved species the range spans from -5 to 35% under increasing CO_2 and from -10 to 10% under constant CO_2 in most environmental zones with the exception of stronger negative changes in the Mediterranean Mountains for European beech and the oaks in Lusitania. Coniferous stands show a large variability in NPP change and mostly positive median NPP changes in the different environmental zones. The NPP change of broad-leaved species is less variable and negative median NPP changes occur under constant CO_2 in the majority of the environmental zones. The regional patterns are comparable in between the species, with a (slightly) decreasing trend in NPP change from north to south.

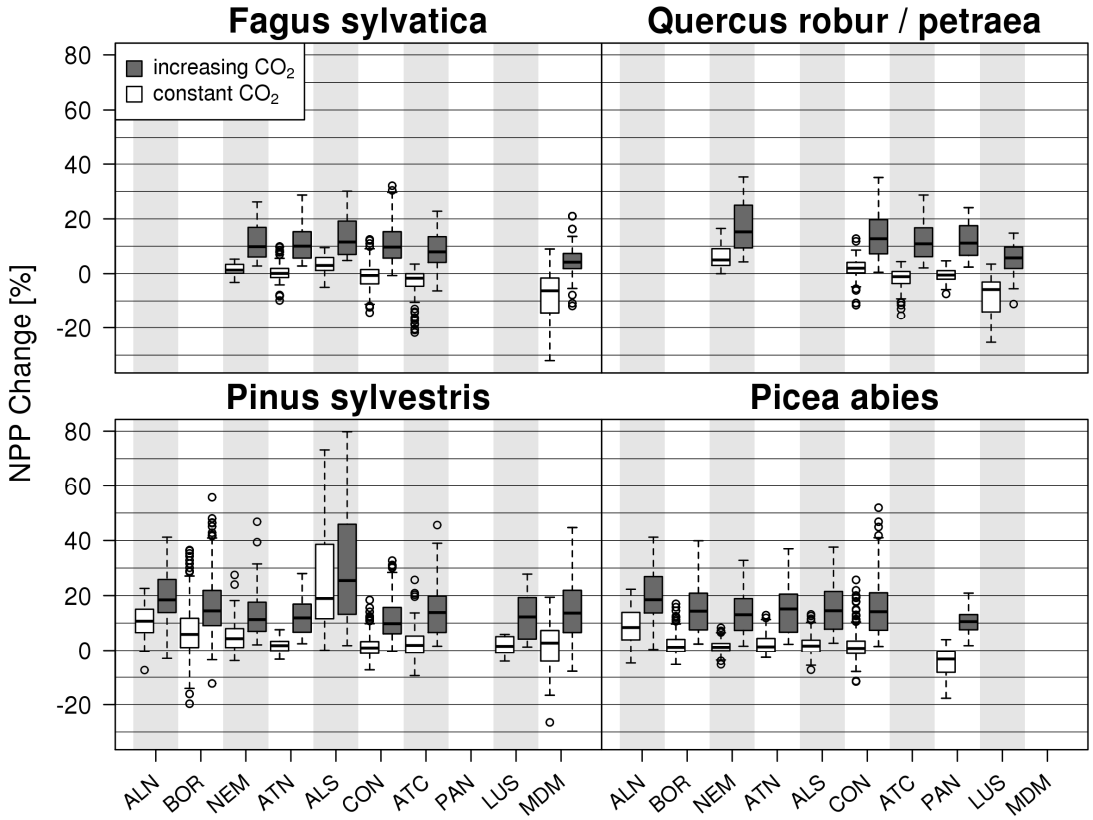

Fig. 3-3 Change in net primary productivity (NPP) for each tree species in each environmental zone (Metzger et al. 2005, for abbreviations see Table 3-1) over all scenarios for simulations with constant and increasing CO_2.

3.4 Discussion

This paper shows that forest productivity in Europe is likely to change under climate change but that the exact amount and partly even the direction of this change depends very much on the choice of the climate change scenario (hence the severity and pace of climate change) and on the persistence of CO_2-effects on forest productivity. There have already been a considerable number of model studies investigating forest productivity changes under climate change at the forest stand scale (e.g. review in Reyer et al. in prep.). The present study complements other European studies in many important aspects: We use typical, existing forest stands which have a defined age, density, site and climate and represent the current species composition as driven by past forest management rather than the potential natural vegetation. We also simulate tree species rather than plant functional types which is usually done in applications at such a large scale (e.g. by Morales et al. 2007). Furthermore, we apply the same model all over Europe, for a large number of stands and for several tree species, which is not common for stand-scale PBMs (e.g. Kellomäki & Leinonen 2005). Additionally, our results are regionalized using detailed environmental zones according to Metzger et al. (2005). Finally, we explicitly consider uncertainties of CO_2-effects on forest productivity by simulating constant and increasing CO_2 which embraces the upper and lower range of the physiological response to CO_2 respectively (Ainsworth & Long 2005; Pinkard et al. 2010). The most closely related study to date has been carried out by Wamelink et al. (2009) which used a similar set of forest stands. However, also in comparison with this study there are several important methodological differences: Firstly, we use a mechanistic formulation of photosynthesis at a weekly resolution to calculate NPP and not annual scaling factors which allows us to include CO_2 and water limitation effects on weekly photosynthesis. Secondly, our approach includes effects of climate change on growing season length and hence of feedbacks such as a longer growing season inducing a longer period of carbon assimilation and exposure to increasing concentrations of CO_2 leading to higher productivity but also to higher risk of soil water depletion already comparably early in the vegetation period and subsequent productivity losses. Thirdly, we did not calibrate 4C on biomass or any other data from the Level-II database. Fourthly, we use several climate change scenarios to assess climate change scenario uncertainties. The climate change scenarios were generated by three different RCMs and then bias-corrected for temperature and precipitation and interpolated to the sites. This shows that our study is unique in its approach. Despite these methodological differences it is valuable to compare

our results with other studies to assess if our study corroborates or contradicts earlier efforts.

3.4.1 NPP changes in Europe

Wamelink et al. (2009) analyzed the change in carbon sequestration under the A2 CO_2-emission scenario until 2070 on a similar set of Level-II sites and found a comparable pattern of stronger changes in productivity in the north than in the south. In their analysis, the importance of a changing climate was however larger and the importance of increasing CO_2 lower probably since they used the A2 CO_2-emission scenario which features stronger changes in climate but also due to their different formulation of CO_2-effects on productivity (see discussion above). Although studying slightly different time periods, regions and climate change scenarios, Morales et al. (2007) found similar magnitudes of NPP change and similar regional pattern as this study. They also identified Southwestern Europe as the most sensitive region, while increases in NPP are strongest in Northern Europe and in the Alps. Qualitatively, our results are also comparable to those of model studies using even more different datasets and modeling approaches (e.g. Milne & van Oijen 2005; Eggers et al. 2008).

Our results are also in line with evidence from data-driven analyses and show that changes in productivity observed in the past are likely to continue. A review by Boisvenue & Running (2006) found that several studies show increasing productivity in temperate and boreal Europe. Vayreda et al. (2012) found that the northern/ north-western mountain areas of the Iberian Peninsula which are dominated by boreal and temperate tree species at the edge of their distribution range are already showing negative effects of warmer temperatures. Our results project these trends to continue although their magnitude depends strongly on the persistence of CO_2-effects.

3.4.2 NPP changes at the species level

At first sight, the good performance of Norway spruce trees in terms of projected NPP changes in this study seems to partly contradict current assessments of Norway spruce's vulnerability to climate change. Other studies for example highlight the strong sensitivity of Norway spruce to climate change in Central Europe (e.g. Kölling et al. 2009). This is however a matter of plot selection. Five of the selected Norway spruce plots feature a mean annual temperature above 8°C and an annual precipitation sum lower than 800mm in the period 1971-2000 (a threshold considered by Kölling et al. (2009) to indicate warm-dry Norway

spruce forests which are especially vulnerable). For these plots, the 4C simulations actually show decreasing productivity in most of the three climate change time slices under constant CO_2 – thus confirming the concerns about Norway spruce's vulnerability to climate change. Many of the remaining Norway spruce stands are located in Northern Europe, where growing conditions are more favorable for Norway spruce. Although Scots pine is generally considered more robust against a changing climate than Norway spruce there are also concerns about Scots pine decline at extreme sites and at the southern limit of its distribution (Rebetez & Dobbertin 2004; Reich & Oleksyn 2008; Galiano et al. 2010) which are also apparent in our results if the simulations under constant CO_2 are considered.

The stands dominated by European beech and oak in our dataset show decreasing NPP under some climate change scenarios. This finding is in line with observations of beech decline in Southern Europe (Jump et al. 2006; Piovesan et al. 2008). However, in general European beech is considered as competitive and climate-resilient in Central Europe (Ammer et al. 2005) although a positive growth response depends on a multitude of environmental and site factors (Geßler et al. 2007). Regarding the responses of oak to climate change in our dataset, it is important to note that the number of oak stands available for our analysis is considerably lower than for the other tree species and this may induce strong sensitivities of the response to extreme sites and climate.

In general the different responses of coniferous and broadleaved species in our study are partly explained by the geographical distribution of the Level-II plots. There are more broadleaved stands located in environmental zones where climate conditions become very warm and much drier while many of the coniferous stands are located in Northern Europe where conditions for forest growth even improve. This does not preclude that we find decreasing productivity for all tree species, mostly under the more severe climate change scenarios towards the end of the century and under constant CO_2.

3.4.3 Climate change scenario uncertainties

One important element of this study was to highlight important uncertainties of the projections of climate change impacts on forest productivity. Thus, the application of several climate change scenarios from different climate models as well as the use of different CO_2-emission scenarios is a crucial component of our assessment since the variation in between climate models has been found to be higher than in between different CO_2-emission scenarios driving one climate model (e.g. Buisson et al. 2010). Our results confirm the findings of Morales et al. (2007) that the effects of using different climate models are more

important than the choice of the CO_2-emission scenario. This emphasizes the importance to rely on scenarios of several climate models in order to provide a more complete picture of plausible future changes in forest productivity.

3.4.4 Persistence of CO_2-effects

While we did not consider model parameter uncertainty in this study, we stress one crucial element of model structural uncertainty throughout our study: the effect of CO_2. Increasing CO_2 enhances productivity through CO_2-fertilization and increasing water-use efficiency (Körner 2006). In 4C, the CO_2-effects on photosynthesis are modeled according to a modified version of Haxeltine & Prentice (1996)'s photosynthesis model which captures well the direct effects of CO_2 on photosynthesis at the leaf level. There is however uncertainty about the long-term persistence of this effect and its implications for forest growth at the forest stand scale (Körner et al. 2005; Norby et al. 2010; Penuelas et al. 2011). For the 20th century, using a similar modeling approach Bellassen et al. (2011) find a very strong importance of CO_2 as driver of increasing forest productivity followed by climate, while the forest age structure contributed only to a much smaller extent. Keenan et al. (2011) also found strong differences between driving a process-based model with increasing or constant CO_2. This pattern is also obvious in our results. Negative effects of climate change on productivity are almost entirely overruled under increasing CO_2. This leads to an increasing divergence of productivity changes throughout the 21st century: Under increasing CO_2, productivity increases more towards the end of the century, while under constant CO_2, productivity decreases more towards the end of the century (see also Fig. 9-13 to Fig. 9-18). This pattern is consistent throughout most of Europe, besides at some sites in Southern Europe with strongly decreasing precipitation. For these sites, decreasing productivity under climate change is very likely and has already been observed (see discussion above). Furthermore, the CO_2-effects level out geographic differences in NPP changes, an effect also emphasized by Bellassen et al. (2011) who highlight the homogenous effect of CO_2 on NPP across Europe as opposed to local climatic trends. To conclude, it is important to note that there is no fully accepted mechanistic formulation of how to model the effects of CO_2 in process-based models that provide results from the leaf- to the stand-level. Acclimation of physiological processes to elevated CO_2 and temperature and nutrient limitation (Lukac et al. 2010) may dampen the strong effects simulated with 4C. Moreover, CO_2-induced higher growth rates are associated with shorter life span of the trees (Bugmann & Bigler 2011; di Filippo et al. 2012) an effect not accounted for in 4C. Therefore, we recommend considering the range of

results from our simulations using constant and increasing CO_2 as a range of possible developments of forest productivity.

3.4.5 Effects not included in this study

There are also other effects on forest productivity that have not been considered in this study. We did not include the effects of nitrogen deposition on forest productivity since although having been important in the past (de Vries et al. 2006; Solberg et al. 2009), the future role of nitrogen depositions is debated (Churkina et al. 2007; Kahle et al. 2008; Reay et al. 2008). Including different assumptions about future nitrogen deposition similarly to the assumptions about CO_2 included in this study would be interesting for future assessments of changing forest productivity. Also, we did not consider age-class effects in our simulations, since we believe that the Level-II stands used here are typical for European conditions and will remain so for the next decades. Ultimately, it is important to note that this study only considers physiological effects of climate change and CO_2 and does not include changing management practices or disturbances which are however likely to be affected by climate change and socioeconomic developments.

3.4.6 Implications for carbon cycling and forest management

Ultimately our results are relevant for a better assessment of both the European carbon cycle and forest management under changing environmental conditions. Although a majority of the climate change scenarios used here may not entail far-reaching changes in forest productivity, our results show that some scenarios may lead to decreasing or increasing productivity and subsequent alterations of the carbon uptake of Europe's forests. This may strongly impact the mitigation potential but also the provision of timber and other ecosystem services of Europe's forests. Forest managers have to cope with this uncertainty and possibly adapt forest management planning by incorporating risk-spreading and adaptive management approaches.

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Landschaft, Wien. Mr. Ferdinand Kristöfel; Belgium (Research Institute for Nature and Forest, Ministère de la Région Wallonne and Mathieu Jonard in particular); Czech Republic (Forestry and Game Management Research Institute, VULHM); Estonia (Estonian Environment Information Centre); Finland (Finnish Forest Research Institute, METLA); France (Ministère de l'agriculture et de la pêche); Germany (Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg, Bayerische Landesanstalt für Wald und Forstwirtschaft, Landesforstanstalt Eberswalde, Nordwestdeutsche Forstliche Versuchsanstalt, Ministerium für Landwirtschaft, Umwelt und Verbraucherschutz Schwerin, Landesamt für Natur, Umwelt und Verbraucherschutz NRW, Forschungsanstalt für Waldökologie und Forstwirtschaft Rheinland-Pfalz, Ministerium für Umwelt, Energie und Verkehr, Landesamt für Umwelt- und Arbeitsschutz Saarbrücken, Staatsbetrieb Sachsenforst, Thüringer Landesanstalt für Wald, Jagd u. Fischerei); Hungary (State Forest Service); Italy (Corpo Forestale dello Stato– Servizio CONECOFOR); Lithuania (State Forest Survey Service); The Netherlands (Ministry of Agriculture, Nature and Food Quality); Norway (Norwegian Forest and Landscape Institute); Poland (Forest Research Institute); Romania (Forest Research and Management Institute, ICAS); Slovak Republic (National Forest Centre); Spain (Forest Health Unit (SPCAN) / DG Nature and Forest Policy (DGMNyPF) / Ministerio de Medio Ambiente, y Medio Rural y Marino); Sweden (Swedish Forest Agency); Switzerland (Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, WSL). Data collection and evaluations were co-financed under the LIFE+ Regulation (EC) 614/2007 of the European Parliament and of the Council. We also would like to thank Beate Klöcking providing us data for the validation. We greatly acknowledge the provision of the CRUPIK dataset by Peter Werner and Herman Österle, the NORDFLUX data by Pasi Kolari and the many people contributing to the Euroflux database. Furthermore, Niklaus Zimmermann, Pedro Contro, Michael Benken, Julia Marusczyk and Alexandra Wilke greatly supported the data preparation for the 4C application. We thank Marc Metzger and Marcus Lindner for providing us the environmental zones of Europe data. The ENSEMBLES data used in this work was funded by the EU FP6 Integrated Project ENSEMBLES (Contract number 505539) whose support is gratefully acknowledged. We are grateful to the IT-services of the Potsdam Institute for Climate Impact Research for providing excellent computational infrastructure to carry out this study. All authors acknowledge funding from the EC FP7 MOTIVE project (grant agreement no. 226544).

4 Integrating parameter uncertainty of a process-based model in assessments of climate change effects on forest productivity[3]

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Abstract

The parameter uncertainty of process-based models has received little attention in climate change impact studies. This paper aims to integrate parameter uncertainty into simulations of climate change impacts on forest net primary productivity (NPP). We assessed the effect of parameter uncertainty on projections of the process-based model 4C in Scots pine (*Pinus sylvestris*) stands under climate change. We compared the uncertainty induced by using climate scenarios from an ensemble of climate change models with the uncertainty induced by parameter uncertainties and climate change together. This paper shows that simulated changes in NPP induced by climate change and parameter uncertainty can be substantially higher than NPP changes induced by climate change alone. It also highlights that the direction of NPP change is mostly consistent between the simulations using the standard parameter setting of 4C and the majority of the simulations including parameter uncertainty. Climate change impact studies that do not consider parameter uncertainty may be appropriate for projecting directions of change but not for quantifying the exact degree of change. This finding is highly relevant since most climate change impact studies do not integrate parameter uncertainty and may thus be over- or underestimating climate change impacts on forest ecosystems.

Keywords: 4C, Bayesian calibration, Climate change scenarios, Europe, Monte Carlo analysis, National Forest Inventory data

4.1 Introduction

Process-based models (PBMs) are important tools in forest and ecological science and widely used to assess the impacts of climate change on forest ecosystems (Landsberg 2003; Fontes et al. 2010). However, their results depend on the reliability of the input data (henceforth referred to as *input uncertainty*), the representation of processes (henceforth referred to as *structural uncertainty*) and the uncertainty about model parameter values (henceforth referred to as *parameter uncertainty*). All these uncertainties need to be accounted for when interpreting the results of model simulations (Cipra 2000).

Besides more 'conventional' input uncertainties due to measurement errors of weather data for example, one type of input uncertainty in climate change impacts studies is the inherent uncertainty about future climate development. Uncertainty in climate scenarios arises from different greenhouse gas emission storylines and from differences between climate models even if driven with the same greenhouse gas emission scenario (e.g. Buisson et al. 2010). This can be partly addressed by using climate change scenario data from several emission scenarios but also by using results from multi-model studies (i.e. an ensemble of climate models).

In many cases parameter values of PBMs are uncertain since they are derived from few and very specific ecophysiological measurements (Mäkelä et al. 2000). This leads to considerable parameter uncertainty especially if a model is applied to sites across the distribution range of a tree species in which phenotypic and genotypic variation prevail. For example, carbon balance models from stand-scale forest growth models (e.g. Valentine 1985; Mäkelä 1986) to dynamic global vegetation models (e.g. Sitch et al. 2003) often include the pipe model (Shinozaki et al. 1964a, b). These models assume that the leaf to sapwood area ratio, which is a central component of the pipe model, is constant for a particular species or plant functional type. However, observational studies show that this ratio varies with climate (Mencuccini & Grace 1995), stand density and site fertility (Espinosa-Bancalari et al. 1987; Long & Smith 1988; Pothier & Margolis 1991; Berninger et al. 2005). If this variation is included in a model, it influences the model results by altering the allocation of net primary productivity to the stem (Berninger & Nikinmaa 1997). While the effects of input uncertainty and of structural uncertainty have been partly addressed elsewhere (e.g. Medlyn et al. 2011; Reyer et al. submitted) and although there are methods that use widely available data sources to address uncertain parameter values (van Oijen et al. 2005; Hartig et al. 2012; van Oijen et al. 2013), parameter uncertainty has received less attention in climate change impact studies.

Therefore, the objective of this paper is (1) to combine analysis of parameter uncertainty with simulation studies of climate change impacts on forest productivity using a process-based forest model and (2) to compare the effects of input uncertainty arising from using several climate change scenarios alone with the effects of both input and parameter uncertainty. This should help to assess the failure of model studies which do not include parameter uncertainty in productivity change estimation under climate change.

We used Bayesian calibration, implemented using a Markov Chain Monte Carlo algorithm, to assess the effects of parameter uncertainty on the projections of the process-based forest model 4C in Scots pine (*Pinus sylvestris*) stands under climate change in Austria, Belgium, Estonia and Finland. More specifically, we calibrated the model parameters of 4C in two different ways: for each country separately and for all countries simultaneously. Thereby two types of parameter distribution were derived: country-specific (calibrated on the stands available in the country) and generic (calibrated on the stands available from all four countries). These distributions were used to test whether calibration improved the model predictions in comparison to the standard, uncalibrated parameter set. We assessed the prior (before calibration) and posterior (after calibration) model output uncertainty for past conditions. Finally, we compared the uncertainty of NPP projections induced by using climate data from an ensemble of climate change models including the uncertainty induced by parameter variations with the uncertainty of NPP projections excluding parameter variations.

4.2 Material and methods

4.2.1 The model 4C

The model 4C ('FORESEE' - Forest Ecosystems in a Changing Environment) describes forest development under changing environmental conditions in a process-based way (Bugmann et al. 1997; Lasch et al. 2005). The processes are modeled on the tree- and stand-level and are based on results from eco-physiological experiments, long term observations and physiological modeling. 4C includes descriptions of ecosystem carbon and water balances, leaf area index and forest structure. Establishment, growth and mortality are explicitly modeled on a patch on which horizontal homogeneity is assumed. The soil sub-model describes temperature and water, carbon and nitrogen dynamics in different soil layers. 4C requires meteorological driving forces at daily resolution as well as a soil and a forest stand description. It is currently parameterized for 11 tree species. Each tree species is

represented by a set of species-specific parameter values. These parameter values originate from literature, aggregated datasets and expert assessment and are henceforth referred to as the standard parameter values (Table 9-8). A more detailed description of 4C, recent model applications as well as a model validation can be found in Reyer et al. (submitted).

To carry out the Bayesian calibration as well as the Monte Carlo simulations, we coupled 4C with the generic and model-independent simulation environment SimEnv (Flechsig et al. 2005, 2012). SimEnv is a multi-run simulation environment that allows for sensitivity and uncertainty analyses of large-volume and multivariate simulation model output in high-dimensional model parameter spaces. It comes with a simple model interface, pre-defined experiment types with probabilistic and deterministic sampling schemes, and experiment analyses and result visualization tools.

4.2.2 Data

In this study, we used data from four European countries where Scots pine is part of commercial forestry, namely Austria (A), Belgium (B), Estonia (E) and Finland (F) (Table 4-1). In each country, two plots from national forest inventories (NFI, e.g. referred to as A1 and A2) and one permanent sampling plot (PSP, e.g. referred to as A3) were available from van Oijen et al. (2013). In Estonia, no NFI plots but three PSPs were available. Hence for the first two of them the data were prepared as if originating from NFI to assure consistency with the other countries. The management of all stands was mimicked by removing trees following a thinning from above management strategy until the measured tree number was reached. A detailed description of the stand, climate and soil data we used for the validation and calibration runs can be found in van Oijen et al. (2013).

For the climate change simulations we used the same soil and stand data but also modeled past climate data to ensure compatibility between past and future model simulations. We prepared data from three Regional Climate Models (RCMs) driven by three different General Circulation Models (GCMs) using the A1B emission scenario (Nakicenovic et al. 2000). The RCM/GCM combinations were CCLM/ECHAM5, HadRM3/HadCM3 and HIRHAM3/Arpège. The data of the latter two RCM/GCM combinations originated from the ENSEMBLES project (van der Linen and Mitchell 2009) while the CCLM/ECHAM5 data were from Lautenschläger et al. (2009a-d). For bias correction and interpolation of the simulated climate data to the sites we followed the same approach as described in Reyer et al. (submitted). A summary of the changes in temperature and precipitation featured in each scenario and at each plot can be found in Table 4-2.

Table 4-1 General information of the stands used in this study. The data refers to the last measurement at each plot. For more information see van Oijen et al. (2013). NFI = National Forest Inventory; PSP = Permanent Sampling Plot; DBH = Diameter at Breast Height.

Site code	Data type	Lat.	Long.	Age [y]	Stem number [ha^{-1}]	Height [m]	DBH [cm]
A1	NFI	48.31°	14.79°	~64	526	18.5	32.4
A2	NFI	48.51°	15.70°	~66	1363	17.7	20.7
A3	PSP	48.51°	15.70°	59	690	18.1	23.9
B1	NFI	51.28°	5.52°	67	380	18.4	27.1
B2	NFI	51.28°	5.52°	66	393	23.2	29.3
B3	PSP	51.3°	4.52°	79	362	21.3	31.9
E1	PSP*	57.85°	25.92°	70	402	25.0	27.4
E2	PSP*	57.98°	25.63°	67	692	24.9	23.7
E3	PSP	57.58°	25.28°	73	667	25.6	24.5
F1	NFI	61.97°	27.67°	75	899	17.8	19.1
F2	NFI	63.83°	24.65°	55	1067	10.1	14.6
F3	PSP	61.33°	25.03°	79	1710	21.8	17

*PSP-data but presented in the format of and used as if originating from NFI data

Table 4-2 Mean annual temperature (T) and mean annual precipitation sum (P) of the periods 1971-2000 and 2061-2090 for three RCMs forced with the A1B emission scenario at the four permanent sampling plots (A3, B3, E3, F3) used in this study.

RCM	Period	T	P	T	P	T	P	T	P
		[°C]	[mm]	[°C]	[mm]	[°C]	[mm]	[°C]	[mm]
		A3		*B3*		*E3*		*F3*	
CCLM	1971-2000	10.0	607	10.5	806	6.1	684	4.4	638
HadRM3	1971-2000	10.0	643	10.3	873	5.9	729	4.0	689
HIRHAM3	1971-2000	10.2	584	10.4	832	6.2	713	4.5	675
CCLM	2061-2090	12.9	605	13.0	852	9.2	787	7.8	718
HadRM3	2061-2090	14.0	635	13.6	809	10.4	734	8.4	739
HIRHAM3	2061-2090	11.7	647	12.1	700	8.9	642	8.1	670

4.2.3 Overview of methodology

This study builds upon a recent model comparison study where national forest inventory (NFI) data were used to calibrate forest models of different complexity in Austria, Belgium, Estonia and Finland (van Oijen et al. 2013). Van Oijen et al. (2013) calibrated parameter distributions of six models with Bayesian calibration techniques. They used either country-specific data from two NFI plots in each country (henceforth referred to as country-specific posterior parameter distribution) or a generic dataset consisting of the data of all the available NFI plots for that study (i.e. eight plots from four countries, henceforth referred to as generic posterior parameter distribution). Including also uncalibrated (i.e. prior) parameter distributions, they aimed to determine whether the models predicted the data of a third plot (a PSP) in each country better without calibration or with the country-specific or the generic calibration. For more details on and formal descriptions of Bayesian calibration and applications with forest PBMs see van Oijen et al. (2005), van Oijen et al. (2011) and van Oijen et al. (2013).

Here, we firstly compared the simulation results of the prior, the country-specific posterior and the generic posterior parameter distributions of the 4C model with the PSP data of van Oijen et al. (2013) in more detail to assess the influence of the country-specific and generic calibration datasets. Secondly, we combined the different parameter distributions with climate change scenarios from three regional climate models to assess the uncertainty of NPP projections induced by an ensemble of climate change projections. Thirdly, we compare this climate change-induced uncertainty in NPP projections with the uncertainty induced by climate change and parameter uncertainties. Fig. 4-1 provides a schematic overview of the methodology and the steps of the analysis.

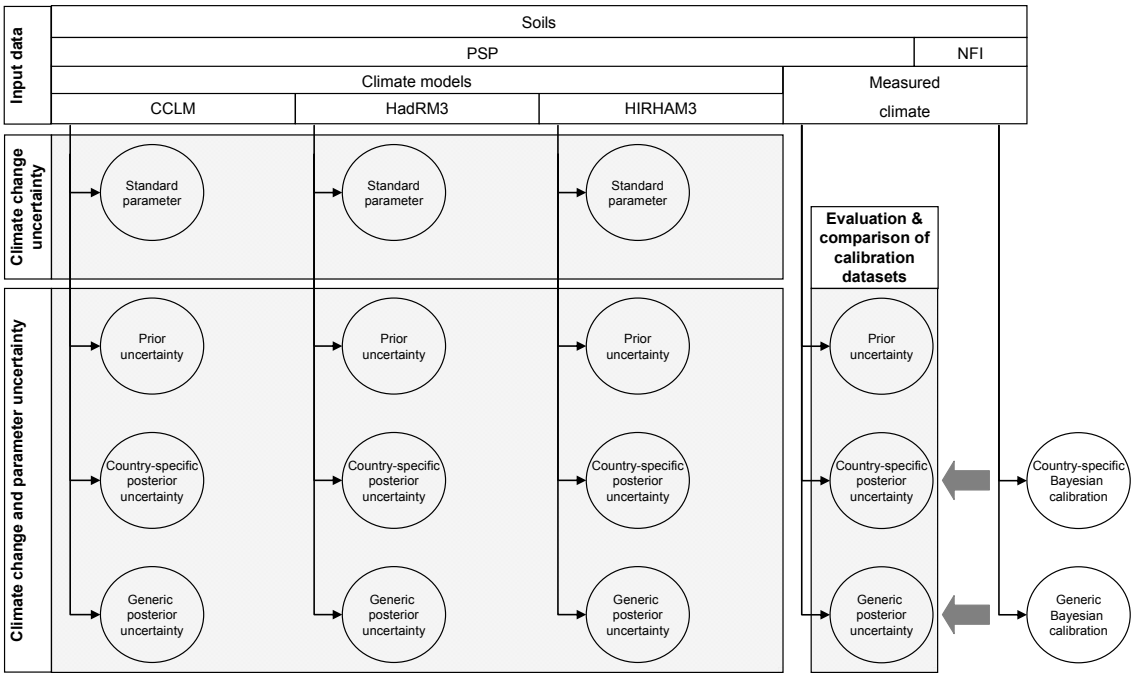

Fig. 4-1 Schematic overview of the methodology and the steps of the analysis (PSP = Permanent sampling plot; NFI = National Forest Inventory). The grey shaded areas represent aspects analyzed in this paper.

4.2.4 Evaluation and comparison of calibration datasets

The prior (i.e. uncalibrated) parameter distribution is a joint distribution consisting of marginal distributions of the individual model parameters. Each parameter was assumed to be uniformly distributed between 50% and 150% of its standard value in 4C (Table 9-8). This ±50% range of parameter values reflects a large uncertainty about parameter values across the broad variety of geographic distribution, stands, sites and climates considered in this study. Using Latin hypercube sampling, we then sampled 1000 parameter vectors from the prior parameter distribution and ran 4C for each parameter vector with the measured soil, stand, management and climate data for a period from the first to the last available data point. This yielded 1000 simulation results that express the prior model output uncertainty

under current climate. To test the sensitivity of our results to the choice of the parameter uncertainty range of ±50%, we also repeated these simulations assuming a smaller uncertainty of initial parameter values of ±25% variation.

The prior parameter distribution assuming a parameter uncertainty of ±50% was then updated during the country-specific (with data from the two NFI plots in each country) and generic (with all available data from the NFI plots in the four countries) calibrations. This resulted in a country-specific and a generic posterior parameter distribution. From each of these we sampled another 1000 parameter vectors and ran 4C with each parameter vector with the measured soil, stand, management and climate data for a period from the first to the last available data point. The results of these 1000 simulations express the country-specific and generic posterior model output uncertainty respectively under current climate.

To assess how the simulations fitted the observed stand data and which calibration dataset improved the predictions the most, we compared observed and simulated mean tree height and diameter at breast height (DBH) for each plot. We calculated the Normalized Root Mean Square Error (NMRSE), based on the whole distribution (i.e. calculated as an average across the samples from the probability distributions) (van Oijen et al. 2013).

4.2.5 Influence of climate change and parameter uncertainty

For the climate change simulations, we ran 4C with the 1000 prior, country-specific posterior and generic posterior parameter vectors as well as with the standard parameter values at each of the four PSPs in the four countries using the measured stand, management and soil data but 30 years of climatic data from the three climate models for the periods 1971-2000 and 2061-2090. Although the changes in climate are driven by an increase in atmospheric CO_2 according to the A1B storyline in our simulations (see section 4.2.2), we kept CO_2 concentration as driving force for photosynthesis constant at 350ppm in this study to separate effects of increasing CO_2 on productivity from climatic effects (see Reyer et al. (submitted) for a more thorough discussion of CO_2-effects). To assess the effects of climate change, we analyzed the change in the mean NPP for the period 2061-2090 compared to the period 1971-2000. This resulted in a total of 96 096 simulation runs (three GCM/RCMs times two time periods times four stands times four parameter distributions based on two priors and two posteriors times 1001 parameter vectors).

To assess the uncertainties induced by the ensemble of climate change scenarios and by parameter uncertainty, we considered the results of the simulations with standard

parameter values and of the full range of simulations with prior, country-specific posterior and generic posterior parameter distributions respectively. We compared the climate change-induced uncertainty with the combined climate change and parameter-induced uncertainty at the European scale because this is actually the scale at which the parameter uncertainty we assume persists. This means that the parameter variation by ±50% or by ±25% does not necessarily occur within a stand but over larger gradients of climate, management etc.

4.3 Results

4.3.1 Evaluation and comparison of calibration datasets

Table 4-3 shows that even without calibration, 4C simulates height and DBH with low NRSME except for F3. As expected, the calibration improves the model results as expressed by a lower NRMSE at all sites and for both diameter and height. The results of the generic calibration fit the data best (with the exception of height at E3) but generally the NRMSE for both calibration datasets are small and similar.

Table 4-3 Normalized Root Mean Square Error (NRMSE) from simulations compared to measured heights and DBHs (Diameter at Breast Height) at four permanent sampling plots in four European countries without calibration and with country-specific and generic calibration.

Site	Uncalibrated	Country-specific calibration	Generic calibration
		Height	
A3	0.29	0.15	0.12
B3	0.23	0.15	0.09
E3	0.13	0.12	0.14
F3	0.52	0.28	0.27
		DBH	
A3	0.23	0.16	0.13
B3	0.14	0.13	0.08
E3	0.06	0.06	0.05
F3	1.00	0.68	0.52

4.3.2 Influence of climate change and parameter uncertainty

Across the four plots used in this study and across the three climate change scenarios, climate change leads to NPP changes ranging from -9 to 29% during the period 2061-2090 relative to 1971-2000 (Fig. 4-2). In the two Central European locations (Austria and Belgium) the responses are mostly small but negative, while in the two Northern European locations (Estonia and Finland) the responses are positive. When parameter uncertainty is included in the climate change simulations, the range of possible NPP changes increases, varying from -44 to 139%, from -46 to 141% and from -45 to 231% for the prior, the posterior generic and

the posterior country-specific model output distribution respectively, but the median changes remain comparable (Fig. 4-2). The two different assumptions about parameter uncertainty, namely ±50% and ±25%, do not lead to large differences in median and the lower and the upper quartiles of NPP change. However, the NPP changes are less extreme under a parameter uncertainty of ±25% and only range from -24 to 94%. There is no large difference between calibrated and uncalibrated model output distributions but overall, the posterior model output uncertainty is slightly larger than the prior output model uncertainty.

Fig. 4-3 shows the relative NPP changes at each of the four plots used in this study split up per regional climate model. In most cases, the NPP change induced by climate change uncertainty alone is consistent with the median of the NPP change induced by climate change and parameter uncertainty. The medians and interquartile ranges of the prior and posterior model output distributions are similar for the same RCM. They differ however between the different RCMs.

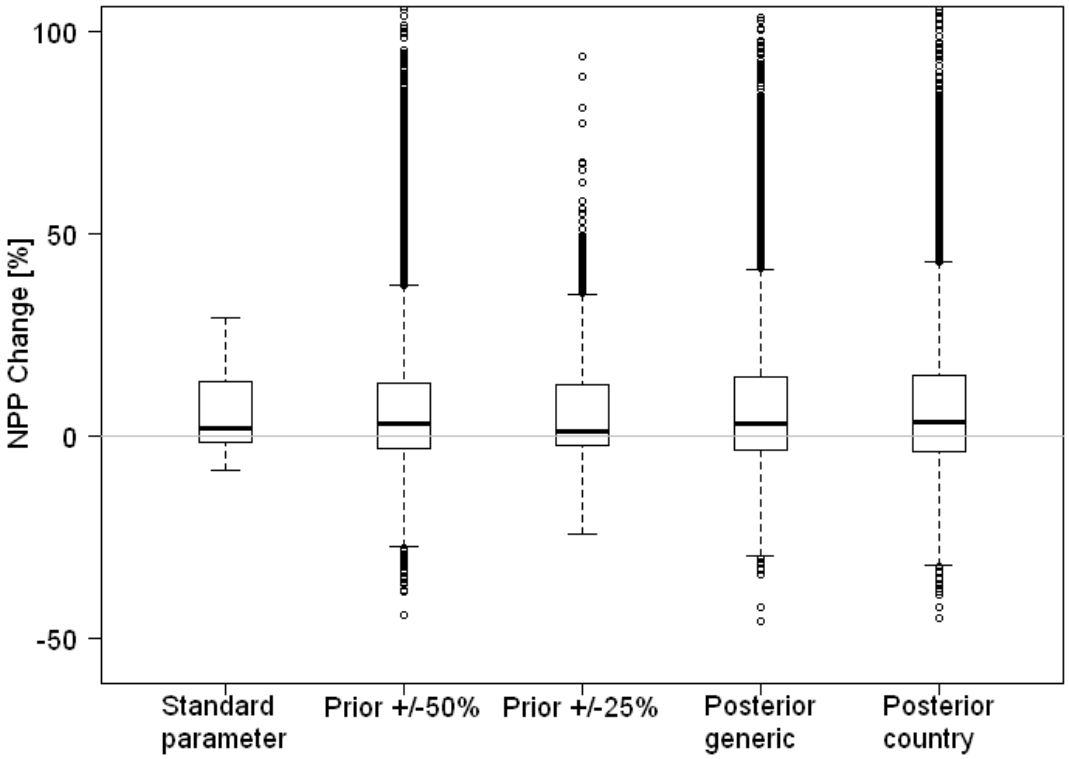

Fig. 4-2 Change in net primary productivity (NPP) across four plots in Austria, Belgium, Estonia and Finland (A3-F3, see Table 4-1) due to climate change alone (Label 'Standard parameter' (i.e. using 4C's standard parameter set and three different climate change scenarios resulting in 12 values)) and due to climate change and parameter uncertainty of uncalibrated (two degrees of prior parameter uncertainty, 'Prior ±50%' or 'Prior ±25%', respectively) or calibrated ('Posterior generic' or 'Posterior country') parameter distributions (each containing 12000 values). See the text for further explanation. The y-axis is cut at 100% for better legibility. The boxplots show the following information: thick line= median, bottom and top of the box = 25th and 75th percentiles, whiskers = maximum value or 1.5 times the interquartile range of the data depending on which is smaller. Points = outliers larger than 1.5 times interquartile range.

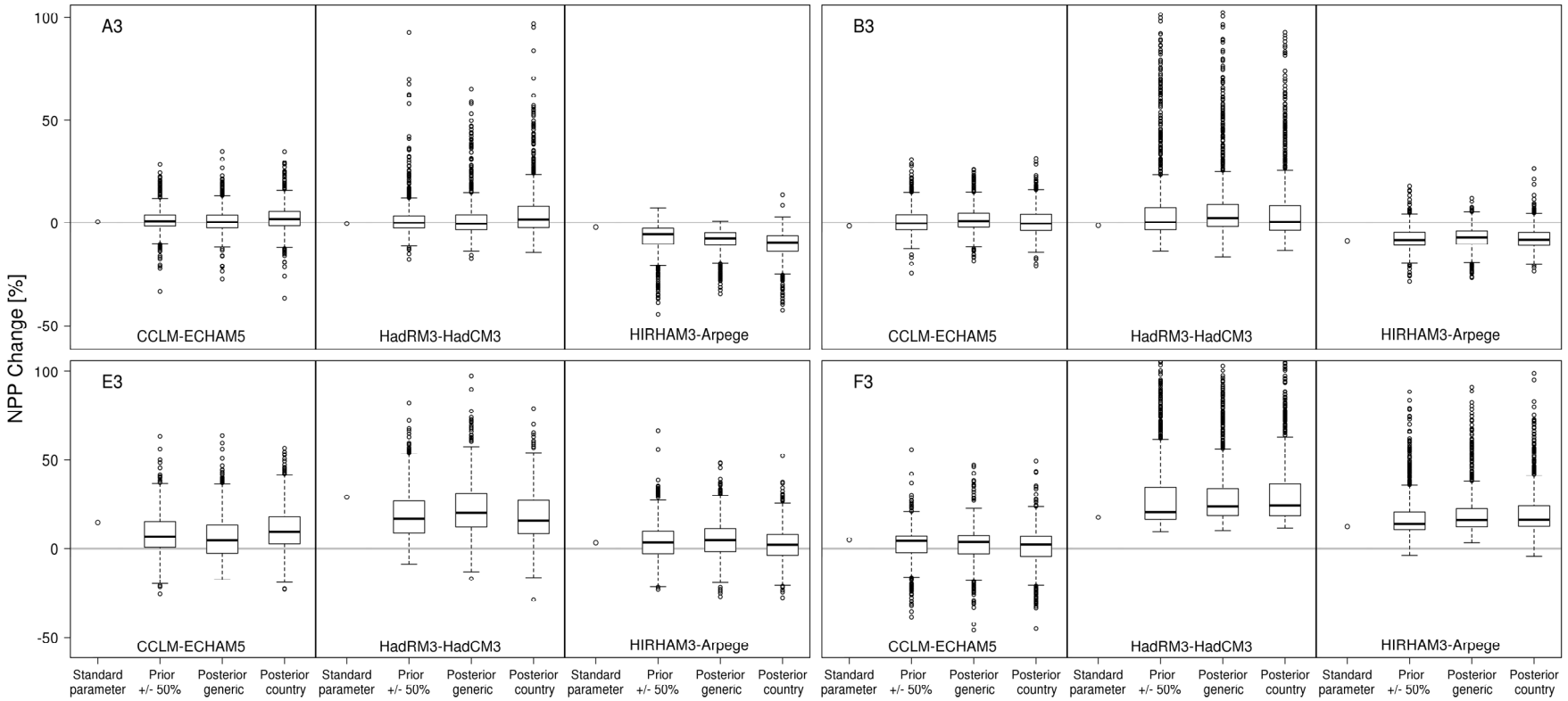

Fig. 4-3 Change in net primary productivity (NPP) at four plots in Austria, Belgium, Estonia and Finland (A3-F3, see Table 4-1) due to climate change alone (Label 'Standard parameter' (i.e. using 4C's standard parameter set)) and due to climate change and parameter uncertainty of uncalibrated ('Prior ±50%') or calibrated ('Posterior generic' or 'Posterior country') parameter distributions. The responses are split up for each climate change scenario. See the text for further explanation. The y-axis is cut at 100% for better legibility. Boxplots as defined in Fig. 4-2.

4.4 Discussion

4.4.1 Evaluation and comparison of calibration datasets

This paper shows that calibration of model parameters with even small amounts of NFI data helped to reduce the NRMSE of height and diameter predictions of a parameter-rich, process-based forest model driven with observed climate (Table 4-3). This is expressed by a low NRMSE of simulations using observed climate. In a recent model comparison study using the same data, 4C was identified as the most plausible model for simulating height and DBH after calibration (van Oijen et al. 2013). Despite a number of limitations (e.g. number of data points and assumptions about the prior parameter distribution), our findings supports evidence from other studies that Bayesian methods combined with NFI data improve model parameterizations which allows for better model performance in comparison with observed data and underlines their importance for sustainability assessments (Mäkelä et al. 2012; van Oijen et al. 2013). Although the generic posterior parameter distribution yielded mostly lower NRMSE values than the country-specific posterior parameter distribution, there were no large differences between the two methods. This is noteworthy since the country-specific posterior parameter distribution included fewer data points. Thus, the advantage of having more data points in the generic calibration was partly compensated for by having country-specific data points in the country-specific calibration.

4.4.2 Influence of climate change and parameter uncertainty

This paper highlights that the uncertainty about changes in NPP induced by climate change and parameter uncertainty can be substantially higher than the uncertainty about NPP changes induced by climate change alone. This means that climate change-induced changes in NPP and its implications for carbon cycling and forest growth may be more uncertain than previously thought and that recently observed productivity increases (e.g. Boisvenue & Running 2006; MacMahon et al. 2010) but also productivity decreases (e.g. Kint et al. 2012) in temperate and boreal forests may amplify in the future. Our findings partly rely on the assumption that the climate change uncertainty induced by the three climate models and the prior parameter uncertainty are realistic and hence comparable.

It is clear that some parameter values may be more, others less variable than the ±50% variation we assumed here (especially in regional applications). Also, the distribution of the prior may differ from a uniform distribution. However, here we took a simple uniform distribution and assumed the same variation for each parameter as a first attempt to

account for parameter uncertainty. The variation around the standard parameter as well as the shape of the prior parameter distribution could be refined in future studies by gathering information of possible parameter values from the literature. A brief, exemplary review on the variation of leaf to sapwood area ratios, which is an important parameter for the allocation submodel, highlights that the 4C standard value as well as its variation by ±50% is well within the range of values found across Europe by Berninger & Nikinmaa (1997), Berninger et al. (2005) and Mencuccini & Grace (1995).

To test however how sensitive our prior model output uncertainties are to the assumption of ±50% parameter variation, we included results from the Monte Carlo simulations without calibration assuming only ±25% variation around the standard value. In this case, the uncertainties about the NPP changes due to climate change and parameter uncertainty were reduced (Fig. 4-2). However, they were still considerably larger than the NPP changes induced by climate change alone and although the extreme values were reduced substantially, the interquartile range of NPP change was almost as large as under the simulations using the ±50% parameter uncertainty. Thus, our results are robust across a large range of assumed parameter uncertainties. Furthermore, the use of posterior parameter distributions corroborates the importance of parameter-induced uncertainty for NPP projections under climate change.

Another important assumption of our study is that the range of climate change scenarios represents a range of possible climate changes. The projections of the RCMs used here range from 1.5 to 4.5°C warming and from -16 to 15% changes in precipitation in between the different stands (Table 4-2) which is well in line with the range of global warming projected by the IPCC for Europe for a similar period (IPCC 2007a). Assuming less warming is probably unrealistic, while more warming would most likely affect our results, so that with stronger warming we expect larger NPP changes and hence a larger climate change-induced uncertainty. Similarly, including increasing CO_2-effects on productivity would probably increase the range of climate change-induced uncertainty (but also in the simulations including parameter uncertainty). Thus, while being conservative, the uncertainty in climate input introduced by the three RCMs seems variable enough to be compared with the uncertainty induced by the variation of parameter values. It is noteworthy that the input uncertainty induced by the different climate change scenarios alone already leads to a variation in NPP changes from 3 to 29% in the most extreme case of E3. Thus, already the input uncertainty has a considerable influence on projections of climate change impacts (cf. Reyer et al. submitted).

Our results reveal one more interesting particularity: Fig. 4-2 and Fig. 4-3 show that the posterior model output uncertainty (of both the generic and country-specific posterior parameter distributions) is in most cases larger than the prior model output uncertainty. This is counterintuitive since for the simulations using measured climate in the first part of our analysis, the posterior model output uncertainty was reduced in comparison to the prior model output uncertainty as indicated by the reduced NRMSE values. The posterior parameter uncertainty was slightly reduced as well. For most marginal parameter distributions the posterior standard deviation was 1-2% less than the prior standard deviation (results not shown). This means that forward propagation of posterior parameter uncertainty to model output uncertainty (of NPP change) leads to increased uncertainty when comparing the effects of multiple climate change scenarios. Hence, the posterior parameter distribution assigns higher probability to a subregion of parameter space where climate sensitivity is high and varies much. This is possible because in 4C, NPP is nonlinearly related to the model parameters.

4.4.3 Implications for climate change impact studies

This paper shows that – while the absolute magnitude of climate change-induced NPP changes is highly uncertain if considering parameter uncertainties – the direction of NPP change is mostly consistent between the simulations using the standard parameter setting of 4C and the majority of the simulations using the parameter variation induced by prior or posterior parameter uncertainties (as expressed by the boxes in Fig. 4-3 which include 50% of the data). Fig. 4-3 shows that typically the median of the NPP change due to climate change and parameter uncertainty mirrors the NPP change induced by climate change alone. Although projections using the standard parameters of 4C do not take into account parameter uncertainty, the direction and quality of change (i.e. small or large) are met quite well. Thus, the standard parameters may be appropriate for projecting directions of climate change impacts especially if including some information on input uncertainty but less their exact magnitude. This increases the confidence in the overall pattern of NPP change under climate change found in recent applications of 4C at the European scale (Reyer et al. submitted). However, it is important that for quantitative assessments of climate change impacts on forests using complex PBMs a more thorough consideration of parameter uncertainty is necessary since parameter uncertainty may outweigh input uncertainty induced by climate change scenarios (which can already be quite large itself). This finding is highly relevant since most climate change impact studies do not integrate parameter

uncertainty and may thus be over- or underestimating climate change impacts on forest ecosystems and may not provide the full range of uncertainties to decision makers. Ultimately, integrating different kinds of uncertainties would allow increasing the robustness of climate change impact studies.

4.5 Acknowledgements

We are grateful to the organizers of the conference 'Tackling climate change: the contribution of forest scientific knowledge' and the editors of this special issue to give us the opportunity to present this research. The COST Action FP0603 and their organizers are acknowledged for supporting the workshops that facilitated the use of Bayesian methods. This work would not have been possible without the data and support provided by Werner Rammer (Austria), Gaby Deckmyn (Belgium), Andres Kiviste (Estonia), Annikki Mäkelä and Sanna Härkönen (Finland). The IT-services team of PIK provided excellent support for this computationally intensive study. We further acknowledge the help and support of our colleagues Felicitas Suckow, Tobias Pilz and Martin Gutsch. CR and PLB acknowledge funding from the EC FP7 MOTIVE project (grant agreement no. 226544).

5 Bayesian calibration, comparison and averaging of six forest models, using data from Scots pine stands across Europe[4]

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Abstract

Forest management requires prediction of forest growth, but there is no general agreement about which models best predict growth, how to quantify model parameters, and how to assess the uncertainty of model predictions. In this paper, we show how Bayesian calibration (BC), Bayesian model comparison (BMC) and Bayesian model averaging (BMA) can help address these issues. We used six models, ranging from simple parameter-sparse models to complex process-based models: 3PG, 4C, ANAFORE, BASFOR, BRIDGING and FORMIND. For each model, the initial degree of uncertainty about parameter values was expressed in a prior probability distribution. Inventory data for Scots pine on tree height and diameter, with estimates of measurement uncertainty, were assembled for twelve sites, from four countries: Austria, Belgium, Estonia and Finland. From each country, we used data from two sites of the National Forest Inventories (NFIs), and one Permanent Sample Plot (PSP). The models were calibrated using the NFI-data and tested against the PSP-data. Calibration was done both per country and for all countries simultaneously, thus yielding country-specific and generic parameter distributions. We assessed model performance by sampling from prior and posterior distributions and comparing the growth predictions of these samples to the observations at the PSPs. We found that BC reduced uncertainties strongly in all but the most complex model. Surprisingly, country-specific BC did not lead to clearly better within-country predictions than generic BC. BMC identified the BRIDGING model, which is of intermediate complexity, as the most plausible model before calibration, with 4C taking its place after calibration. In this BMC, model plausibility was quantified as the relative probability of a model being correct given the information in the PSP-data. We discuss how the method of model initialization affects model performance. Finally, we show how BMA affords a robust way of predicting forest growth that accounts for both parametric and model structural uncertainty.

Keywords: Dynamic modeling, Forest management models, Growth prediction, National forest inventories, Permanent sample plots, Uncertainty

5.1 Introduction

Ecological models are built for a variety of purposes. One general motivation is trying to integrate our understanding of the processes underlying natural phenomena. At a time when the earth system is subject to substantial changes in land use and climate, however, it also becomes of increasing importance to be able to make quantitative predictions, supported by a quantification of uncertainty, about the future of our ecosystems.

Forest ecosystems are a prominent example where quantitative predictions are of particular ecological and economic importance, but for which there is considerable uncertainty because different modeling approaches, models and parameters are available (Mäkelä et al. 2012). We focus here on weather-sensitive dynamic models, which simulate the growth of forest stands over time. Dynamic models that have been considered for forest management range from fairly simple, parameter-sparse empirical models to complex models with many parameters (Fontes et al. 2010). None of these models has found widespread application across Europe, which may be due to problems of parameterization and a lack of knowledge about the generalisability of the models. Given the increasing availability of forest data from National Forest Inventories (NFIs) and Permanent Sample Plots (PSPs), and other data sources, however, it can be hoped that limitations of dynamic forest models with respect to data availability can be substantially reduced in the future (Hartig et al. 2012). These data can help in parameterization and evaluation of the models, if we can find robust ways of comparing models and accounting for measurement and modeling uncertainties. In this paper, we use methods based on probability theory, more specifically Bayesian calibration (BC), Bayesian model comparison (BMC) and Bayesian model averaging (BMA), to address these issues. A strength of these methods is that they can be applied to any type of model. Although we do restrict our focus here to dynamic, weather-sensitive models, we have included models of widely differing structure, complexity and data needs, providing a broad practical test of the methods.

Bayesian methods have been used before to calibrate the parameter distributions of dynamic forest models, starting with the work of Green et al. (1999), but application to parameter-rich process-based models is still rare (Luo et al. 2009). The use of BMC to compare and evaluate dynamic forest models – or any other vegetation models – is a more recent application. Van Oijen et al. (2011) included BMC in their analysis of four models for forest biogeochemistry and Fu et al. (2012) used BMC to identify the most plausible models for predicting tree budburst. Here we present, as far as we know, the first applications of BMC and BMA to dynamic forest growth models that include both parameter-sparse semi-

empirical models and complex process-based models with many parameters. Using NFI- and PSP-data on Scots pine (*Pinus sylvestris* L.) from four European countries, we compared the results of calibration and testing of these models using the combined dataset with the results where the same methods were applied to within-country data only. The purpose of this was to assess whether the models would be most effectively calibrated and applied at smaller or larger spatial scales. Similar comparisons of Bayesian approaches applied locally and generically have been made for a simple soil ionic concentration model by Reinds et al. (2008) and for a model of N_2O-emissions in crops by Lehuger et al. (2009).

We ask the following questions:

- How effective are local stand data in reducing uncertainties about forest model parameters in a Bayesian framework?
- Are the considered dynamic models for Scots pine sufficiently general to allow a generic calibration to data from across Europe, or should models be calibrated on a country-by-country basis?
- How effective is Bayesian model comparison in identifying plausible predictive models, and what are the main distinguishing characteristics of forest models that are selected?
- Does Bayesian model averaging lead to improved predictions compared to individually calibrated models?

Although these questions, as well as the models and data used, are focused on forestry in Europe, our methodology is unrestrictedly general. BC, BMC and BMA, and the contrasts made between within- and cross-country applications, can be applied to any other combination of data sets and models in the environmental sciences.

5.2 Materials and methods

5.2.1 Overview of methodology

Our study used six models and 12 data sets which originated from forest measurements in four European countries (Table 5-1). The data were from National Forest Inventory (NFI) sites and from sites with Permanent Sample Plots (PSPs). From all sites we retrieved environmental data (weather, soil and management) and tree growth data (height and diameter). These data were used by all models to the extent of each model's input data

requirements (Table 5-2). Fig. 5-1 is a flow chart that shows how the data were used in the consecutive stages of the study. The environmental data from the NFI-sites were used as drivers for model application to those sites. Each model was run multiple times for each NFI-site, to assess the impact of parameter uncertainty on model outputs. We refer to this step as 'prior uncertainty quantification' (prior UQ) because no data of tree growth had been used at this point for improvement of parameter values. The distributions of model outputs generated by this prior UQ were used in a Bayesian model comparison (prior BMC) to quantify the relative plausibility of each model before calibration. These differences in model plausibility were then used as weights in Bayesian model averaging (BMA), thus producing an averaged prediction to which all six models contributed differently. Next, the NFI-data were used for Bayesian calibration of the parameters of the different models. The calibration was carried out both per country and generically using data from all NFI-sites. The calibrated models were then applied to the PSP-sites using local environmental data. At this stage, we again carried out uncertainty quantification, now termed 'posterior UQ' because the model parameter distributions were already informed by the NFI-data. Finally, the results from the posterior UQ were compared with measurements from the PSP-sites for a posterior Bayesian model comparison, again accompanied by BMA. In the rest of this section, we describe data, models and statistical methods in more detail.

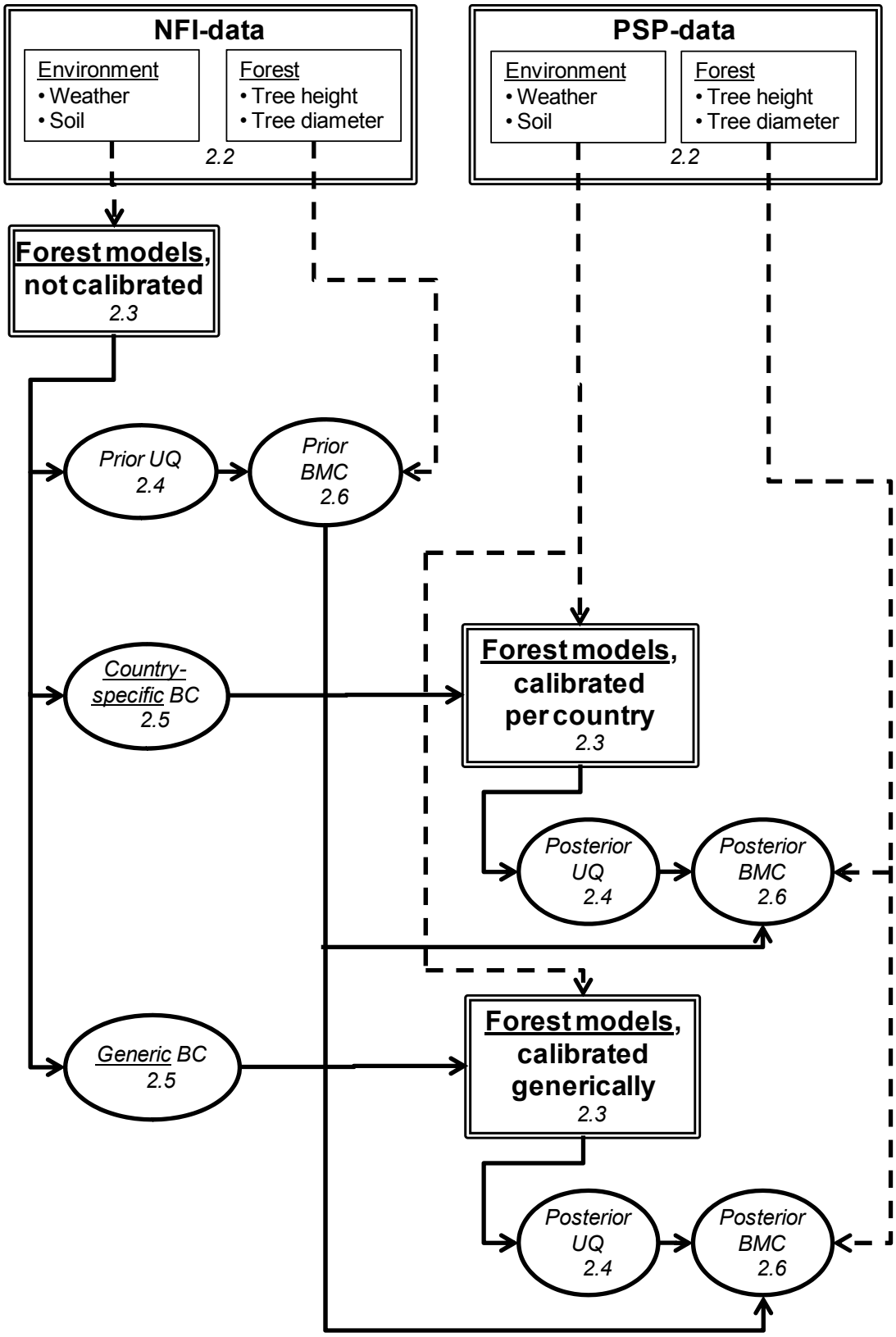

Fig. 5-1 Flow chart of the study. The numbers within icons (2.2-2.6) indicate in which paragraph of section 5.2 further explanation of can be found.

5.2.2 Data

Data of twelve even-aged *P. sylvestris* stands were assembled from four European countries (Table 5-1). From each country, two NFI sites and one PSP-site were selected for this study. An exception was Estonia, for which NFI-data were not available and three PSPs were used. For ease of reference, we used a site-code for each site consisting of the first letter of the country's name, followed by one or two for the NFI-sites and three for the PSP-site (Table 5-1), except for Estonia where the numbers refer to the three PSPs. For model calibration, we only used data from the sites coded one or two, whereas for model comparison and averaging the data from sites with code number three were used. The data used were for mean tree height and stem diameter at 1.3m above ground, which were available from all sites. Data on stem number and tree age were used as uncalibrated inputs. All sites provided several measurements for the different variables (between two and seven), separated by intervals of at least 5 years (Fig. 5-2). We now briefly describe the sites in each country.

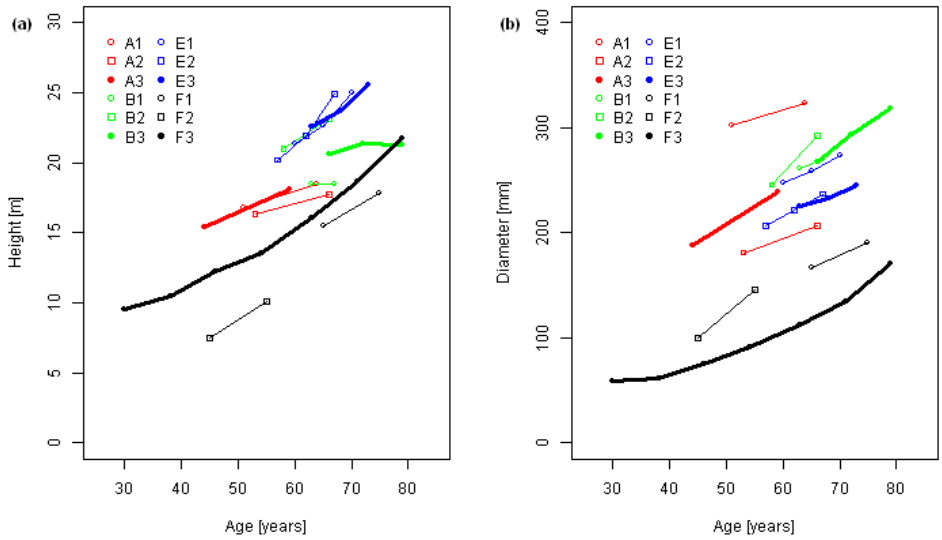

Fig. 5-2 (a) Mean tree height vs. stand age as observed at the twelve forest sites. (b) Idem for stem diameter. Site-codes (A1 … F3) are explained in Table 5-1.

Austria

The NFI-plots A1 and A2 are part of the Austrian Forest Inventory grid consisting of ~10 000 points. The plots are 100% *P. sylvestris* and the soils are classified as Semipodsol and Cambisol with soil depths exceeding 0.3m and field capacity around 36%. They are located at different altitudes in the 'Waldviertel', a region in Lower Austria north of the Danube. A1 lies about 300m higher than A2 and is cooler and drier. On both sites, measurements were taken in two years (1987 & 2000 and 1989 & 2002). The sample consisted for each plot of a combined angle count measurement (for trees >10.5cm diameter) and a circle with a fixed radius (for trees <10.5cm). Height measurements were done for a subset of trees of the

angle count measurement; the other heights were calculated. Nothing is known about management history or planting time, except that no management occurred during the period of measurements.

The selected PSP-site, A3, was established in 1970 and measured every five years. The site is maintained by the Austrian Federal Forest Office BWF (http://bfw.ac.at/) and is located near A2 with similar soil properties. It is a pure *P. sylvestris* stand with a size of 1500m² and a stem number of 790ha^{-1} in 1980.

Climate data for the NFI- and PSP-sites were provided from nearby weather stations of the Austrian weather service ZAMG (Central Institute for Meteorology and Geodynamics).

All three stands reached heights of about 18m at an age of about 60 years. However, they differ significantly in diameter (207-324mm), with lower values at high stem number.

Belgium

The Belgian plots B1 and B2 are NFI's of the ANB (Agentschap Natuur en Bos, 'Forest and Nature Agency'), situated in the Campine region of north-eastern Belgium, were established in 1937 and 1942 respectively and regularly thinned since then from the original 12 500 trees ha^{-1}. B1 is situated on loamy sand, and data from 2000 and 2004 were available; thinning during this period reduced stem number from 400 to 380ha^{-1}. B2 is situated on sandy soil close to B1 and data from 2000 and 2008 were available. Thinning during this period reduced stem number from 520 to 393ha^{-1}. The data were obtained from 40 times 25m sample plots.

The PSP-site, B3, 'De Inslag', is a mixed patchy coniferous/deciduous forest located in Brasschaat also in the Belgian Campine region. The site is part of the European Carboeurope-IP network and is a Level-II observation plot of the European network program (ICP-II forests) for intensive monitoring of forest ecosystems, managed by the Flemish Research Institute for Nature and Forest (INBO). Here we only focus on one particular even-aged Scots pine stand planted in 1929 and described by Curiel Yuste et al. (2005). In this experimental stand, stem number was 556ha^{-1} in 1997. In November 1999, a thinning was performed reducing the stem number to 377ha^{-1} and further thinned to 362ha^{-1} in 2002. The soil is loamy sand, moderately wet, with a distinct humus and iron B-horizon (Baeyens et al. 1993) and is classified as Umbric Regosol. Although the Belgian plots are on relatively sandy soils, soil water table is quite high (0.7-1.0m) and soil fertility is high due to high nitrogen deposition (30-40 kg N ha^{-1} year^{-1}).

Despite similar age (66-67 years) and stem number (380-390ha^{-1}), the two NFI-plots had quite different heights (18.4 and 23.2m) and diameter (271 and 293mm) indicating differences in site quality. The PSP-site was older and had lower tree number; height was intermediate but diameter was greater than at the NFI-plots.

Estonia

The Estonian plots E1, E2 and E3 belong to the Estonian Forest Research Plots Network which consists of more than 700 PSP and are maintained by the Estonian University of Life Sciences (Sims et al. 2009). These plots were established at the observation sites of the European network programme ICP Forest Level I plots. The plots, established in 2000, are circular with radii of 25, 20 and 25m, respectively and were re-measured in 2005 and 2010. The plots have not been thinned during that period, but earlier management history is unknown. On each plot, the diameter at breast height was assessed for each tree. Tree height and height to crown base were measured in every fifth tree. All three plots are dominated by Scots pine (more than 90% of total volume), but there is a small mixture of Silver birch (*Betula pendula*) and Norway spruce (*Picea abies*). The plots are located in southern Estonia where mean effective temperature sum is about 1650 degree days. The plots are on sandy soils on glaciofluvial deposits with sufficient water availability belonging to WRB 2006 soil units Gleyic Podzol, Histic Podzol and Albic Podzol respectively. The vegetation types of the plots are Rhodococcum, drained Polytrichum-Nyrtillus, and Rhodococcum. The basal area of the plots reached 24.8, 33.7, and 31.8m^2 ha^{-1} at stand ages 70, 67, and 73 years, with average heights of 25.2, 24.7, and 25.6 m and volumes of 285, 384, and 374m^3 ha^{-1}. Differences in diameter (237-274mm) were larger than height differences, with largest values reached at the lowest stem number.

Finland

The Finnish plots F1 and F2 are permanent NFI sample plots located in Southern Finland established by the Finnish Forest Research Institute. They have been measured in 1985 and 1995. The plots have not been thinned during that period. The earlier treatment history is unknown. The plot size varied according to the stem diameter at breast height, being 100m^2 when the diameter was under 10.5cm, and otherwise 300m^2. The trees with diameter smaller than 4.5cm were measured only if they were expected to survive until the next measuring date. Diameter at breast height and tree species were recorded from all the tally trees. Heights, crown base heights and crown widths were measured from the sample trees,

which include the trees that were located in a circular area around the sample plot mid-point, where the circle radius is half of the original sample plot radius.

The Finnish plot F3 is a control plot with no thinnings in a permanent thinning experiment of the Forest Research Institute at Vesijako in southern Finland. The experiment was established in 1948 in a pine stand sown in 1918, and it was followed until 1997. The site is fairly fertile with adequate moisture for pine. The plot has a small mixture of birch (*Betula* spp.), less than 10% of basal area. Plot size was 1000m^2, and all trees were numbered on this plot and measured for breast height diameter in a total of seven measurements. For height (and crown base height in the two most recent measurements), 21-67 trees were chosen as sample trees. The final heights of 17.8m (75 years, NFI 1), 10.1m (55 years, NFI 2) and 21.8m (79 years, PSP) indicate that despite the age difference, the site conditions at NFI 2 were probably less favorable (cf. Fig. 5-2a). The comparatively low stem number and the high diameter, and the fact that no mortality occurred, suggest that the NFI plots were thinned at some point before the surveys. In contrast, at the PSP-site only self-thinning occurred leading to high stem numbers and low diameters.

5.2.3 Models

We used six different forest models in the assessment, ranging from simple semi-empirical models to parameter-rich process-based models (Table 5-2). All models are able to predict mean tree height and mean stem diameter. Some of the models are able to simulate variation between individual trees as well, but the corresponding predictions were not tested against data. Four of the models are initialized at the first measurement date, i.e. they require the earliest observed values of mean tree height and/or diameter to quantify the model's initial constants (Table 5-2). This reduces the number of data available for Bayesian calibration. The remaining two models, 3PG and BASFOR, include state variables that are difficult to estimate from mean height and stem diameter only, such as nitrogen pools in soil and trees, and it was therefore decided to initialize them from planting. These two models therefore have more data available for calibration, but their predictions of forest growth may already start deviating from observations before the first measurement date. We shall now briefly describe each model, referring to earlier publications for more detail. Each model description finishes with an account of how the prior probability distribution for the model's parameters was set by the respective modelers. The role of these probability distributions in uncertainty quantification and Bayesian calibration is explained in the sections 5.2.4 and 5.2.5.

3PG

3PG calculates the dynamics of biomass in different organs (foliage, roots and stem) and simulates the soil water balance and variables of interest to forest managers, such as stand timber volume, mean diameter at breast height, stand basal area and mean annual growth increment. Gross primary production (GPP) is calculated by multiplying photosynthetically active radiation absorbed by the stand with a light-use efficiency that changes with environmental conditions. Light absorption is calculated using Beer's law, while the light-use efficiency varies in dependence of atmospheric vapor pressure deficit, air temperature, the presence of frost, soil water balance, tree age and site fertility. Net primary productivity (NPP) is calculated as a constant fraction of GPP (Waring et al. 1998; Law et al. 2000). Carbon allocation is based on allometric equations, applied on a single-tree basis. The fraction of NPP allocated below-ground decreases with soil fertility. Site fertility is expressed through a site specific reduction factor (FR) that varies between zero (for the least fertile sites) and one (for sites that do not have nutrient limitations). The remaining NPP is partitioned between the aboveground organs as a function of stem diameter at breast height. The diameter at breast height and the average stand height are calculated through allometric functions of average aboveground biomass per tree. 3PG has been applied to various different species and sites and is widely used in research as well as by companies to assess forest growth and site productivity. Detailed descriptions of 3PG were provided by Landsberg & Waring (1997) and Sands & Landsberg (2002).

Before this study, Landsberg et al. (2005) tested the performance of 3PG for Scots pine in Finland, using a modified carbon allocation routine. Xenakis et al. (2008) coupled 3PG with ICBM/2N (Introductory Carbon Balance Model (Andren & Katterer 1997)) a soil matter decomposition model. The new model, 3PGN, was calibrated and tested for Scots pine plantations in Scotland. The information from these two previous studies was utilized to construct the prior, using truncated Gaussian distributions. For each parameter, the prior mean was set to the average of the values used in Landsberg et al. (2005) and Xenakis et al. (2008). The bounds of the prior were set at ±30% of the mean value. The site fertility parameters were also included in the BCs and BMCs; the FRs ranged between zero and one, while the prior mean was 0.5. For all parameters, the prior was kept quite uninformative (i.e. high variance and wide ranges), reflecting the fact that the 3PG-modeller in the current study did not have previous experience with Scots pine.

4C

The forest model 4C (FORESEE –FORESt Ecosystems in a changing Environment) has been developed to simulate the impact of changing environmental conditions on forest ecosystems. It is climate sensitive and calculates physiological processes on the tree and stand level depending on the process in question in daily to yearly time steps (Bugmann et al. 1997; Suckow et al. 2001). Establishment, growth and mortality of tree cohorts are explicitly modeled at the patch scale on which horizontal homogeneity is assumed. Cohorts of trees compete for light, water and nutrients (Bugmann et al. 1997). Every cohort develops specific values for fine root, foliage, stem biomass, etc. and species-specific parameters steer the physiological processes for each species. Photosynthetic rate is calculated after Haxeltine & Prentice (1996) and a constant fraction of GPP is lost to respiration (Landsberg & Waring 1997). The resulting NPP thus depends on environmental conditions and is allocated according to the principles of the pipe model (Shinozaki et al. 1964a) and of the functional balance (Davidson 1969) and organ-specific, constant senescence rates. In this allocation model, height growth is decoupled from diameter growth, with high degrees of intra-canopy shading leading to extra height growth. Nitrogen limitation has been calculated dynamically. When the tree water demand of a cohort exceeds the plant available water in the soil, the canopy conductance and ultimately NPP of that cohort is reduced. 4C requires daily meteorological variables, a soil description including physical and chemical parameters as well as a forest stand description. For further details of model processes and recent model applications, see Suckow et al. (2001), Lasch et al. (2005), Seidl et al. (2008) and Reyer et al. (2010).

The prior distribution for all parameters of 4C was uniform with boundaries at ±50% of the initial (standard 4C) value, reflecting large uncertainty about parameter values. The selection of the parameters to be calibrated was restricted to species-specific parameters that could be informed by Scots Pine data, giving a total of 43 parameters amenable to calibration.

ANAFORE

ANAFORE (ANAlysing FORest Ecosystems) is a stand-scale, mechanistic forest model that dynamically simulates the fluxes of carbon, water and nitrogen through the ecosystem (Deckmyn et al. 2008). The forest stand is described as consisting of trees of different size cohorts (e.g. dominant, co-dominant and suppressed trees), either of the same or of different species (deciduous or coniferous). Half-hourly carbon and water fluxes are modeled at the leaf, tree and stand level from half-hourly, daily or monthly climate data. In

addition to total growth and yield, the model simulates allocation changes in crown size, DBH-height ratio, root-shoot ratio and even the daily evolution of tracheid or vessel biomass and radius, parenchyma and branch development. From these data, early and late wood biomass, wood tissue composition and density are calculated to allow wood quality estimation. Simulation of the labile carbon stored in the living tissues allows for simulation of trans-seasonal and trans-yearly effects, and simulation of the long-term effects of environmental stresses on growth. A detailed soil model including fungal, bacterial and mycorrhizal effects on SOM degradation and aggregate formation is included (Deckmyn et al., 2009). Model initialization was at the first measuring point. Because ANAFORE needs a detailed tree description – not available for most sites – allocation as observed at the Belgian sites was used throughout (% heartwood, branch biomass, crown length). Crown width was set to fill the site.

The prior distribution for the parameters was uniform with boundaries at ±10% of the initial value, reflecting measured data (mainly on the Belgian Brasschaat site) and data from literature as described in Deckmyn et al. (2008). Although ANAFORE was calibrated for Scots pine before this study, this was only for Belgian stands and the uncertainty concerning parameterization across Europe is large, so the same prior was used.

BASFOR

The BASic FORest simulator, BASFOR, is a deterministic daily time step forest model used for simulating coniferous or deciduous forests. The model simulates carbon and nitrogen cycling in trees, soil organic matter and litter. It simulates the response of trees and soil to radiation, temperature, precipitation, humidity, wind speed, atmospheric CO_2 and N-deposition, and thinning regime. The model has 14 state variables, representing carbon and nitrogen pools in trees and soil, and 48 parameters which include the initial constants of the state variables. Besides time series for the state variables, output may be produced of NPP, tree height, stem diameter, ground cover, LAI, N-mineralization and other tree and soil variables. BASFOR is built from well known process representations. Light absorption is calculated by Beer's law. GPP is calculated as light absorption times a light-use efficiency (LUE). NPP is calculated as a fixed ratio of GPP. LUE is temperature-, CO_2- and water-dependent and may be reduced if insufficient nitrogen is taken up by the plants. Potential nitrogen uptake scales with root system surface area. Actual nitrogen uptake is the minimum of demand, determined by tissue N-concentration, and potential uptake. Allocation of assimilates

follows allometric rules, but water stress may limit leaf area index (LAI). Turnover of tree and soil components proceeds at temperature-dependent relative rates.

The model structure was described by Van Oijen et al. (2005), more recent model applications are reported by Van Oijen & Thomson (2010) and Van Oijen et al. (2011), and the model is now also in use as the tree component of an agroforestry model (Van Oijen et al. 2010). The prior for BASFOR was constructed from beta-distributions for the individual parameters, with ranges and modes based on literature as described before (Levy et al. 2004; Van Oijen et al. 2005, 2011).

BRIDGING

The BRIDGING model (Valentine & Mäkelä 2005) was developed to bridge the gap between process-based and empirical approaches to modeling tree growth by formulating a process-based model that can be fitted and applied in an empirical mode. Tree growth in the model is based on carbon balance, and its allocation is consistent with pipe model theory and an optimal control model of crown development (Mäkelä & Sievanen 1992). These provide a framework for expressing the components of tree biomass in terms of tree height, crown height and stem cross-sectional area, the growth of which is regulated by photosynthesis and respiration. The parameters of the model comprise physiological rates and morphological ratios and can be estimated from lower-level process models or direct measurements. In the empirical mode, the original parameters are combined into a set of fewer, aggregate parameters which can be estimated from inventory type data using statistical procedures. Here, we calculate the photosynthesis and respiration parameters from lower-level models of stand productivity (Mäkelä et al. 2008) and canopy structure (Duursma & Mäkelä 2007) using a procedure proposed by Härkönen et al. (2010). The productivity model is driven by daily data of global radiation, vapor pressure deficit and air temperature, while field data on inventory variables (stand-level mean values of height, diameter, crown base height and crown width, stocking density or basal area, and site fertility) are used for parameterizing canopy structure. These parameters are given fixed, deterministic values. The parameters related to growth of tree height and basal area are employed in their aggregate form and estimated using the Bayesian approach with the given inventory data.

The Bridging model has 38 different parameters, of which the 13 parameters relating to the dynamic growth of tree height and basal area were used in the calibration. Uniform distributions were used throughout. Parameters left out of the calibration included

structural relationships, which were calculated directly based on the measured stand data, biomass estimates, and light-use efficiency estimates. The uniform distributions were mainly quantified based on earlier pipe model studies (Mäkelä 1997; Palmroth et al. 1999; Mäkelä & Vanninen 2001; Valentine & Mäkelä 2005; Vanninen & Mäkelä 2005; Duursma & Mäkelä 2007).

FORMIND

FORMIND is an individual-based, spatially semi-explicit gap-type model (Köhler & Huth 1998; Ruger et al. 2007). Spatially semi-explicit means that the modeled plot (in this case 1ha) is divided into 20 times 20m gaps. Tree individuals are assigned to one of these gaps, but do not have an explicit position within gaps. As in classical gap models, tree crowns are assumed to cover the gap uniformly in horizontal direction at a certain height, depending on the size of the trees. The vertical stratification through the different crown heights of the trees and the differences in light climate that result from that for each individual tree are important determinants of the predicted community dynamics. NPP is calculated as the difference between GPP and respiration. GPP of each individual tree depends on the available light at crown top, temperature and soil water content. The temperature dependence follows a hump shape. A reduction due to insufficient soil water occurs below a threshold and GPP is completely reduced if soil water content falls below the permanent wilting point. Additionally, maintenance respiration has a temperature dependence following the Q10-approach (Gutiérrez & Huth 2012). The model was initialized for each site at the first recorded year with the observed number of trees, all of the same observed average diameter, randomly distributed over the modeled area of one hectare.

The marginal prior probability distributions for FORMIND were all uniform. Parameters were excluded from the calibration that were either unrelated to those model outputs that were compared to calibration data, or for which there were other parameters already under calibration that acted on the model outputs in a similar way. Based on this premise, four parameters were selected for calibration. These included the two parameters that determine the diameter-height relationship, the main growth parameter that determines the maximum growth rate under full light, and the wilting point, which is the determinant of how strongly the plants react to water stress. The other parameters were fixed according to literature data. For each of the calibration parameters, flat and relatively wide priors were chosen reflecting large uncertainty about parameter values.

Table 5-1 Data. Each row represents one of the twelve measurement sites. If multiple values of stem number are shown, they refer to changes over the period of measurement. The rightmost column gives the total number of data points at the site, for tree height and diameter combined. T = temperature, P = precipitation.

Country	Site name	Site code	Site type	Lat.	Long.	Plot size [m^{-2}]	Mean T [°C]	Mean P [mm y^{-1}]	Age at last obs. [y]	Stem number [ha^{-1}]	# Data
Austria	Point 1	A1	NFI	48.31°	14.79°	1200	7.6	855	~64	554-526	4
	Point 2	A2	NFI	48.51°	15.70°	1200	9.2	466	~66	1772-1363	4
	PSP	A3	PSP	48.51°	15.70°	1500	9.2	466	59	790-690	4
Belgium	Hechtel	B1	NFI	51°17'	5°31'	1000	9.9	812	67	400-380	4
	Pijnven	B2	NFI	51°17'	5°31'	1000	9.9	819	66	520-393	4
	Brasschaat	B3	PSP	51°18'	4°31'	20000	9.9	811	79	538-362	6
Estonia	EST-1	E1	PSP	57°51'	25°55'	1963	5.4	629	70	428-402	6
	EST-2	E2	PSP	57°59'	25°38'	1257	5.4	632	67	796-692	6
	EST-3	E3	PSP	57°35'	25°17'	1963	5.3	625	73	652-667	6
Finland	NFI-1	F1	NFI	61°58'	27°40'	100-300	2.8	534	75	899	4
	NFI-2	F2	NFI	63°50'	24°39'	100-300	2.2	442	55	1067	4
	Vesijako	F3	PSP	61°20'	25°2'	1000	3.5	521	79	8700-1710	14

Table 5-2 Models. Each row represents one of the six models. The weather variables driving the models include radiation, temperature, precipitation, wind speed and atmospheric humidity (BASFOR), or a subset of those (3PG, 4C, ANAFORE, BRIDGING, FORMIND). The rightmost column shows whether models simulated forest growth from planting or were initialized using the earliest measurements at each site. IBM = Individual-Based Model requiring specification of size and position of each tree.

Model	Time step	Environmental variables	Number of state variables	Number of parameters (# in calibration)	Initialization
3PG	Monthly	Weather	9	51 (48)	Planting date
4C	Daily-Yearly	Weather, Soil conditions, N-deposition, CO_2	15	46 (43)	First measurement
ANAFORE	Half-hourly	Weather, Soil conditions, N-deposition, CO_2	26	146 (138)	First measurement
BASFOR	Daily	Weather, N-deposition, CO_2, Soil conditions	14	48 (41)	Planting date
BRIDGING	Yearly	Weather	5	38 (13)	First measurement
FORMIND	Yearly	Weather	IBM	42 (4)	First measurement

5.2.4 Uncertainty quantification (UQ)

Predictive uncertainty (i.e. uncertainty regarding model outputs) was quantified for each model at three stages in our study: before any parameter calibration had been carried out (prior UQ), and after country-specific and generic calibration (posterior UQ) (Fig. 5-1). In each case, the UQ consisted of running the model 1001 times, using a sample of that length from the parameter distribution for the model.

For each model, the prior parameter uncertainty – before any of the NFI- or PSP-data had been used for calibration – was expressed in the form of a probability distribution. This was done by each modeling group separately, no standardization of priors being attempted (see section 5.2.3). To derive from that the prior predictive uncertainty, we used a sample consisting of the mode of this parameter distribution plus 1000 other parameter vectors sampled from the prior distribution using Latin Hypercube Sampling to ensure good coverage of parameter space. This prior UQ was carried out for all 12 sites.

To assess the posterior predictive uncertainty, i.e. the uncertainty resulting from the reduced parameter uncertainty after country-specific or generic Bayesian calibration (see section 5.2.5), we used the mode of the posterior parameter distribution, i.e. the Maximum A Posteriori (MAP) parameter vector, and again 1000 other parameter vectors that were selected by equidistant subsampling from the parameter chains generated in the calibration. Posterior UQ was carried out only for PSP-sites because the data from those sites had not been used in the calibration.

5.2.5 Bayesian calibration (BC)

Bayesian calibration was carried out as documented in other recent forest model studies (Van Oijen et al. 2005; Van Oijen et al. 2011) and we shall give only a brief outline here. The method starts by expressing uncertainty about the model's parameter values in a so-called prior parameter distribution, $P(\vartheta)$. In this notation, ϑ represents the full parameter vector of a model, so $P(\vartheta)$ is a multivariate distribution. All modelers in this study assigned prior distributions without any correlations between different parameters, so $P(\vartheta)$ could be written as the product of independent distributions for the individual parameters. By comparing model predictions with NFI-data, D, we can derive a likelihood value $P(D|\vartheta)$ for each possible parameter value (see section 2.6), which can be interpreted as a relative 'goodness-of-fit' measure for this parameter (Hartig et al. 2012). Bayes' formula then allows

us to combine both pieces of information (prior and likelihood) into one posterior parameter distribution. The formula states that:

$$P(\vartheta|D) \propto P(\vartheta)\, P(D|\vartheta),$$

i.e. that posterior probability is proportional to prior times likelihood $P(D|\vartheta)$. To derive a likelihood function, we made the assumption, for all models and measurements, that measurement errors were normally distributed with a coefficient of variation of 20%. The fairly high value of 20% was chosen to account for multiple factors affecting the measurements, including instrument error, demographic stochasticity of the tree populations, and environmental heterogeneity. No correlations between measurement errors were assumed, so our likelihood function could be written as the product of independent Gaussian functions of the difference between data D and model output $M(\vartheta)$:

$P(D|\theta)$ = Probability of measurement error equal to D-$M(\vartheta)$

$$= \prod_{i=1}^{n} \varphi(D_i - M_i(\theta); 0, (0.2D_i)^2),$$

where the i-subscripts index the n data points and the corresponding model outputs, and where φ denotes a Gaussian probability density function with given mean and variance.

To estimate the posterior distributions, we used a Markov Chain Monte Carlo (MCMC) algorithm (Metropolis et al. 1953; Van Oijen et al. 2005). Convergence of the MCMC was verified both visually – by inspection of the parameter trace plots – and by calculation of the Gelman-Rubin statistic (Gelman & Rubin 1992).

5.2.6 Bayesian model comparison (BMC) and calculation of NRMSE

Bayesian model comparison relies on the same probabilistic ideas as BC, but now the probability distribution to be informed by the data is not that for the parameters but for the models themselves (Kass & Raftery 1995). A key strength of BMC is that it evaluates models not at one single parameter vector value but takes into account parameter uncertainty (Tuomi et al. 2008). The formal need for this coverage of parameter uncertainty is seen when we write out Bayes' Theorem as applied to model comparison:

$$P(M|D) \propto P(M)\, P(D|M),$$

where following the law of total probability:

$$\mathrm{P}(D|M) = \int P(D \mid M(\theta))\,\mathrm{P}(\theta)\,\mathrm{d}\vartheta.$$

So each model's parameter uncertainty, and not only the best value, determines how much support a model receives. Among other things, this provides a natural safeguard against overfitting using overly flexible models. P(D|M) is referred to as the 'integrated likelihood', or also the 'marginal likelihood' as it is calculated by marginalizing out the uncertain influence of the model's parameters. We assumed that each model had the same prior probability of 1/6 before any data were used. Application of the models to the NFI-sites, in the prior UQ, provided 1000 model results which were used to derive each model's integrated likelihood for those data. The posterior probability for each model was then calculated as the model's integrated likelihood divided by the sum of the integrated likelihoods for all models (Kass & Raftery 1995). A similar procedure was applied at the next applications of BMC, where the integrated likelihoods of the models were calculated for the PSP-data after the models had been calibrated on the NFI-data. These posterior BMC's were carried out after both country-specific and generic BC.

Additionally, we calculated a standard goodness-of-fit measure, the normalized root mean squared error (NRMSE), for model predictions at PSP-sites. This was done for both the prior and posterior parameter distributions. In contrast to the calculation of the integrated likelihood, the NRMSE had to be calculated separately for height and diameter as its calculation involves a normalization by the average of the measurements:

$$\mathrm{NRMSE} = \frac{1}{\overline{D}}\sqrt{\frac{1}{n_c \times 1000}\sum_{c=1}^{n_c}\sum_{\theta=1}^{1000}(M_c(\theta) - D_c)^2}$$

where n_c is the number of countries from which PSP-data were used, D_c are the measured values, $\overline{D}$ is the average of the measurements across the n_c countries, ϑ indexes the 1000 parameter vectors sampled from prior or posterior distribution and $M_c(\vartheta)$ is model prediction for country c using parameter vector ϑ. In the case of the prior and generic posterior parameter distribution, the calculation of NRMSE uses n_c = 4, but in the case of country-specific posteriors, NRMSE is calculated first per country (n_c = 1) followed by averaging of the four errors to arrive at an estimate of overall NRMSE.

5.2.7 Bayesian model averaging (BMA)

Bayesian model averaging uses the different model probabilities P(*M*), derived in preceding BMC, to calculate a weighted probability distribution for model outputs (Kass & Raftery 1995; Hoeting et al. 1999):

$$P(y) = \sum_{m=1}^{6} P(M^{(m)})P(y \mid M^{(m)})$$

where P(*y*) is the averaged output distribution, P($M^{(m)}$) is the probability for model m as derived from the BMC, and P ($y|M^{(m)}$) is the output distribution for model $M^{(m)}$. Expanding the last term gives:

$$P(y) = \sum_{m=1}^{6} P(M^{(m)}) \int P(y \mid M^{(m)}, \theta^{(m)}) P(\theta^{(m)}) d\theta^{(m)},$$

which shows that the BMA accounts for both overall model structural uncertainty, P(M(m)), and each individual model's parameter uncertainty, P(θ(m)). In this study, BMA was applied after both prior and posterior BMC, with P(θ(m)) representing prior and posterior parameter uncertainty, respectively. The same model output samples used in BMC were used for BMA as well, but subsampled with sample size proportional to P(M(m)). The BMA-forecasts thus produced were compared against the measurements at the PSP-sites. Note that in this procedure only the prior BMA was subjected to a fully out-of-sample test of predictive capacity of the model averaging.

5.3 Results

5.3.1 Uncertainty quantification before and after Bayesian calibration

The first quantity calculated was the prior predictive uncertainty, that is, the model uncertainty before any data were used for calibration. Table 5-3 shows summary statistics of the prior predictive distributions for the NFI-sites: the value of mode of the prior plus the 5% and 95% quantiles. Fig. 5-3 and Fig. 5-4 depict the ranges between the 5% and 95% quantiles for the PSP-sites. The prior output ranges – delimited by the 5% and 95% quantiles – were generally widest for the three most parameter-rich models, i.e. ANAFORE, BASFOR and 3PG.

Bayesian calibration (BC) was carried out both per individual country and generically, so samples from five different posterior parameter distributions were produced for each

model. Our results show that generic Bayesian calibration reduced parameter uncertainty in all models except ANAFORE, with average reductions in the standard deviation of marginal parameter distributions (i.e. for individual parameters) ranging from 1 to 13%. These averages were invariably the result of a majority of parameters being hardly affected by the BC and a small number with strongly reduced uncertainty, with maximum reductions in standard deviation for individual parameters ranging from 6 to 83% across all models (data not shown). The results of country-specific BC were similar but with generally lower reductions in uncertainty.

Fig. 5-3 and Fig. 5-4 show predictive uncertainty after calibration for mean height and diameter. With respect to output uncertainty, measured as the distance between the 5% and 95% quantiles, the results for country-specific and generic BC were quite similar (Table 5-3; Fig. 5-3; Fig. 5-4). BC reduced tree height uncertainty in all models, but most in 3PG and BASFOR and least in BRIDGING. For stem diameter, 3PG and BASFOR again saw large uncertainty reductions but otherwise the results differed markedly from those for tree height, with ANAFORE and BRIDGING seeing no clear reductions in predictive uncertainty and FORMIND even becoming worse at B3, E3 and F3.

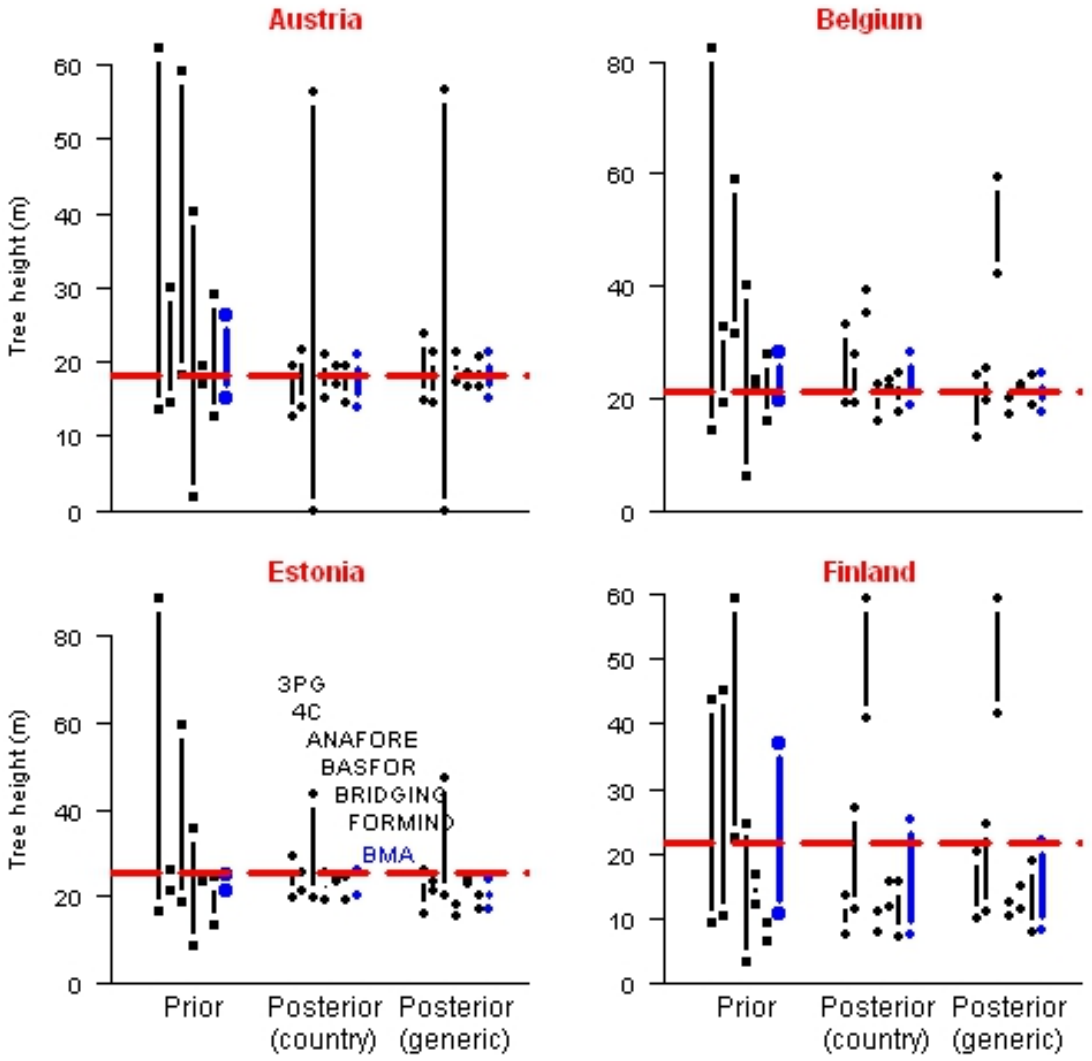

Fig. 5-3 Model output uncertainty for final mean tree height at the PSP-sites A3, B3, E3, F3. Vertical bars show the central 90% of distributions. For each country, the three clusters of bars show prior and posterior (country-specific, generic) predictions. The seven bars in each cluster are for the six models plus the Bayesian Model Averaging result, in the order indicated in the bottom-left panel. The dashed horizontal lines indicate observed values, which were not used for model calibration.

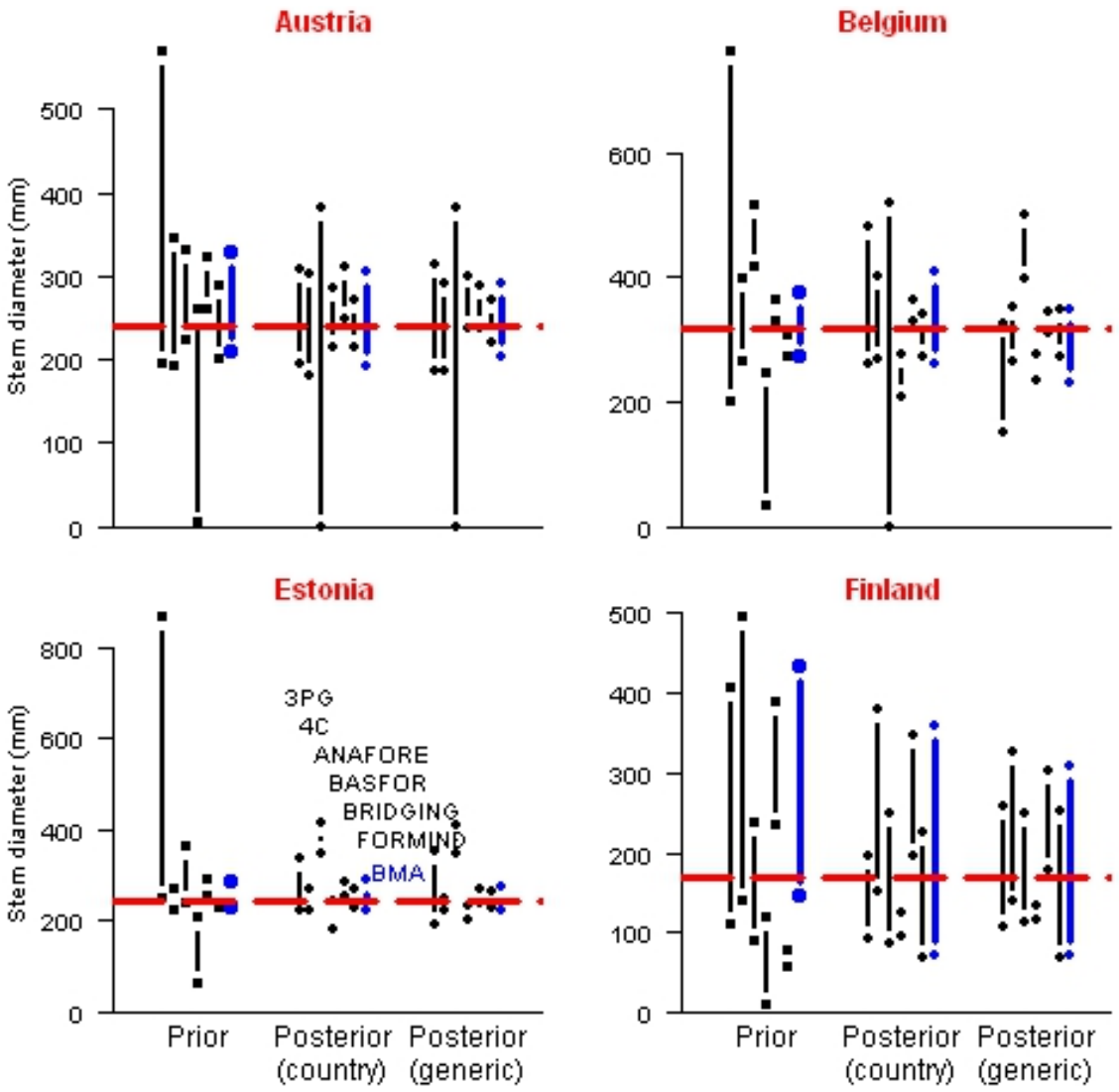

Fig. 5-4 Model output uncertainty for final mean stem diameter at the PSP-sites A3, B3, E3, F3. The lay-out of the figure is the same as for Fig. 5-3.

Table 5-3 Prior predictions by six models of final tree height (m) and stem diameter (mm) on twelve sites. Site-codes (A1, A2, etc.) are explained in Table 5-1. For each combination of model and variable, the first row shows the predictions using the mode of the prior parameter distribution, and the second gives the range (5%-95% quantiles). The upper two rows show the measured values for comparison.

Source	Variable	A1	A2	A3	B1	B2	B3	E1	E2	E3	F1	F2	F3
Data	Height	18.5	17.7	18.1	18.4	23.2	21.3	25.0	24.9	25.6	17.8	10.1	21.8
	Diameter	324	207	239	271	293	319	274	237	245	191	146	170
3PG	Height	52.4	21.0	28.4	28.6	28.8	32.8	40.7	32.7	36.0	30.2	23.5	19.5
		21.3-145	10.7-45.0	13.5-62.1	13.1-66.9	13.5-67.6	14.3-82.2	17.7-102	15.4-78.9	16.3-88.5	14.1-68.0	11.5-47.6	9.3-43.6
	Diameter	622	211	303	301	305	356	462	357	400	325	241	194
		337-1476	140-403	195-568	178-607	188-599	201-760	287-960	227-749	248-865	205-646	156-430	110-407
4C	Height	21.6	20.9	20.7	19.6	23.1	24.5	22.5	20.7	21.8	16.7	12.5	26.0
		15.9-29.1	15.6-27.2	14.3-29.9	17.8-25.0	20.0-30.1	19.2-32.6	20.0-29.3	19.0-25.4	21.3-26.0	14.4-22.2	7.6-20.9	10.2-45.3
	Diameter	381	267	284	287	297	352	288	254	244	205	161	340
		291-430	191-298	191-344	267-305	250-322	263-398	243-320	211-271	224-271	170-233	120-201	139-495
ANAFORE	Height	30.2	27.6	28.5	19.4	25.4	46.9	29.0	28.7	24.7	26.7	20.5	48.0
		23.9-59.2	17.4-59.1	18.3-59.2	18.9-23.1	23.3-33.6	31.4-59.0	18.8-52.0	20.5-51.6	18.5-59.2	20.3-49.5	10.0-46.6	22.4-59.3
	Diameter	457	185	330	309	323	457	471	355	376	280	238	219
		335-481	182-195	222-331	299-323	303-344	417-516	277-426	210-326	241-364	245-314	206-436	89-237
BASFOR	Height	25.9	14.6	18.9	22.5	18.9	21.2	18.0	17.9	19.0	16.4	14.6	13.1
		12.6-48.1	1.4-36.2	1.7-40.2	10.8-41.6	1.4-36.9	5.8-39.9	7.8-33.9	7.8-33.4	8.3-35.6	2.5-31.1	2.2-27.9	3.1-24.7
	Diameter	229	98	144	186	144	170	133	132	145	115	97	82
		131-319	3-221	3-261	103-259	3-220	31-244	52-190	49-189	62-208	6-170	4-143	9-119
BRIDGING	Height	18.2	17.5	18.2	19.2	21.8	22.6	22.7	21.4	23.9	17.5	11.5	12.9
		17.5-18.8	17.0-18.1	17.0-19.4	18.9-19.6	21.5-22.2	22.0-23.2	22.1-23.3	20.9-22.0	23.3-24.5	16.6-18.4	10.0-13.0	12.1-16.8
	Diameter	423	261	305	312	331	353	320	271	279	226	210	265
		375-442	229-273	261-321	296-321	302-349	327-363	290-334	245-282	255-289	200-237	175-225	233-388
FORMIND	Height	26.6	21.0	22.1	22.0	20.9	22.1	20.9	18.5	19.8	16.0	11.0	8.0
		16.0-32.4	12.0-26.3	12.5-29.1	14.8-26.4	15.1-26.0	16.0-27.6	14.3-25.9	13.0-22.7	13.5-24.5	11.2-19.6	8.2-13.1	6.3-9.1
	Diameter	352	251	270	268	250	270	250	210	230	170	100	63
		302-362	190-264	201-288	260-273	250-273	270-305	250-251	210-212	230-232	170-170	100-102	56-78

5.3.2 Bayesian model comparison before and after calibration

The predictions of the uncalibrated models for the NFI-sites, generated as part of the prior UQ reported in the previous paragraph, were compared against the corresponding NFI-data in a prior Bayesian model comparison (BMC) (Fig. 5-5). Despite the fact that the data tended to fall between the 5% and 95% quantiles of each model's prior uncertainty ranges (Table 5-3), the Bayesian model comparison still assigned very different prior probabilities to the different models. The most parameter-rich model, ANAFORE, and the two models initialized at planting, 3PG and BASFOR, had prior probabilities orders of magnitude lower than the other three models. BRIDGING and, to slightly lesser extent, 4C achieved the highest integrated likelihoods (Fig. 5-5).

The posterior BMC, in which models outputs after calibration were compared with measurements at PSP-sites, showed smaller differences between model probabilities and slightly altered the ranking of the models (Fig. 5-5). The posterior BMC assigned the highest probability to 4C, followed by BRIDGING and FORMIND with 3PG thereafter.

Similar ranking can be observed in the values of NRMSE (Fig. 5-6), which like the integrated likelihoods of the models were calculated as averages for the whole parameter distribution. For all models except ANAFORE, the values of NRMSE for mean height and diameter were markedly reduced by BC but with little difference between country-specific and generic BC.

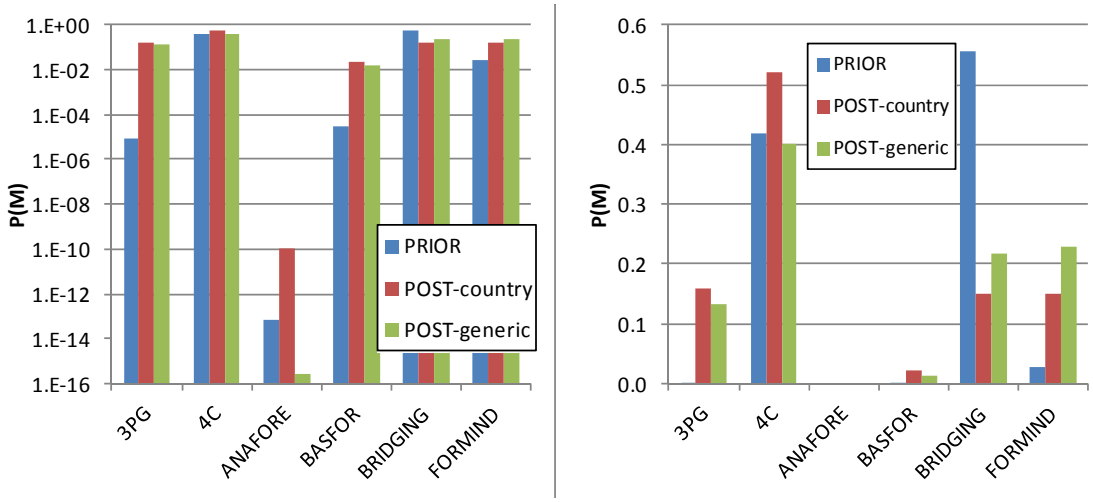

Fig. 5-5 Prior and posterior model probabilities, derived from the integrated likelihoods of NFI and PSP-measurements. Left: logarithmic scale; Right: absolute scale.

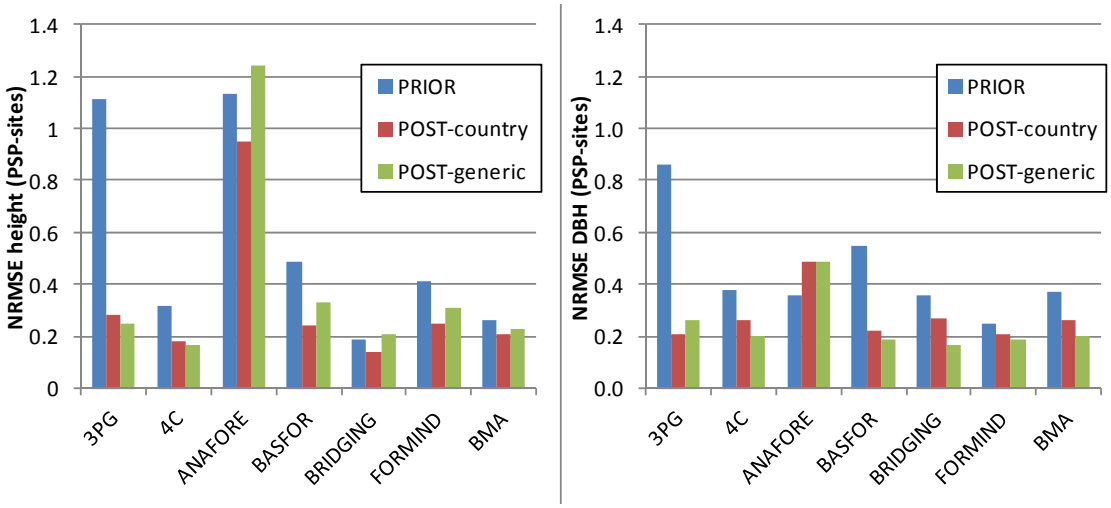

Fig. 5-6 Normalized RMSE, derived from simulations at PSP-sites using samples from prior and posterior parameter distributions. Left: tree height, right: diameter at breast height. The rightmost three bars in both panels are the result of Bayesian Model Averaging (BMA).

5.3.3 Bayesian model averaging before and after calibration

The weighted average predictions of the models for the PSP-sites, using prior and posterior model probabilities as weights, are included in Fig. 5-3, Fig. 5-4 and Fig. 5-6. The prior BMA, which was based on model probabilities derived from NFI-data without any model calibration, showed robust out-of-sample predictive capacity for the PSP-sites, as shown by low NRMSE-values for both output variables (Fig. 5-6). In the case of tree height, only the BRIDGING model had lower NRMSE, whereas for stem diameter only 4C had clearly lower error. Also, predictive uncertainty from the prior BMA was moderate, with at least half of the models showing larger uncertainty ranges for all combinations of variable and site except stem diameter at F3.

Predictions from posterior BMA were also compared against the measurements at PSP-sites (Fig. 5-3; Fig. 5-4; Fig. 5-6). In contrast to the tests of prior BMA, and despite the fact that only NFI-data were used in model calibration, these were in-sample tests of predictive capacity because PSP-data had been used to calculate the model probabilities. Prediction using posterior BMA was less of an improvement compared to most individual models than was the case for prior BMA (Fig. 5-3; Fig. 5-4; Fig. 5-6).

5.4 Discussion

5.4.1 Model performance before and after Bayesian calibration on NFI-data

If forest models are to be useful in management, their predictions must be sufficiently accurate and precise. A quantification of model accuracy for growth is given in Table 5-3, where the predictions for the modes of prior parameter distributions can be compared against measurements. The same table also provides information about predictive uncertainty, in the form of the 5% and 95% quantiles of model predictions. The results show that only the BRIDGING model had high *a priori* predictive accuracy for mean tree height with low accompanying uncertainty at all sites except F3. For stem diameter, none of the uncalibrated models was very precise – BRIDGING, 4C and FORMIND did best – and only BRIDGING and FORMIND had low uncertainties throughout. The balance of accuracy and precision for the NFI-sites was such that the prior Bayesian model comparison assigned 55% prior probability to BRIDGING and 42% to 4C.

One reason for the prior success of BRIDGING and 4C, and to lesser extent FORMIND, was that these models were initialized for each site at the first date of measurement. The models were thus started off with values of mean tree height and stem diameter correct for the site, and with fewer years of growth remaining to be predicted than what was asked from models initialized at planting, such as 3PG and BASFOR. The advantage of late model initialization – having less time to deviate from true on-site growth patterns – apparently weighed heavier than that of 3PG and BASFOR being able to process more detailed information about the site conditions. Furthermore, information about the early management history of sites, such as the tree thinning regime, tends to be less reliable than information for the measurement periods. Late initialization, however, does not always improve predictive performance, as demonstrated by the results for ANAFORE. In the case of ANAFORE, a highly detailed model, there was a large suite of other state variables besides mean height and diameter that needed to be initialized, and for which no good information was available for most sites so default model settings could not be adjusted. While some models may be designed to run with stand-level information such as typically provided by NFIs, other models may perform better if more detailed initialization data are available. In this study, the most complex model, ANAFORE was clearly overparameterized in relation to the very limited data. We also note that BRIDGING and 4C might have been rated best if initialization values would have been estimated rather than being set a priori – but that was not investigated in this study.

These comparisons of the prior performance of the different models were inevitably also affected by how the prior parameter distributions were defined. Different methods for quantifying prior parameter distribution of a process-based forest model, PnET-II, were discussed by Radtke et al. (2001). The prior distributions in our study were set independently by each modeling group, using the information available to them from literature and from previous experience with their model. This partly explains why some models, such as 3PG, showed wider prior output ranges than other models.

To restrict the influence of subjective prior parameterization, it is therefore important to compare differences in model performance after all models have been calibrated for the tree species under study. Both country-specific and generic Bayesian calibration on NFI-data markedly increased the accuracy and precision of prediction for the PSP-sites by all models except the most complex and parameter-rich model, ANAFORE (Fig. 5-3; Fig. 5-4). After these general improvements, the 4C model performed best (Fig. 5-5), but note that the differences in model initialization method again affected the results, and that the strength of the data was probably still not sufficient to completely overrule the effect of prior choice after calibration. Also note that the assessments of model performance and plausibility in this study are restricted to predictions for mean tree height and stem diameter. If data from other variables, such as above-and belowground biomass and wood quality, had been used, model evaluation would likely have yielded different results.

5.4.2 Spatial differences in model performance

All models had the poorest predictions of mean tree height for the Finnish PSP-site. That site, F3, had an atypically high stem number (Table 5-1), which may have contributed to comparatively strong height growth at relatively small diameter despite advanced age (Fig. 5-2). Most models apparently struggled to simulate this growth pattern, irrespective of model complexity. The problems with this site largely persisted after calibration.

Sites within a single country are likely to be more similar in tree provenance, soil type and climate than sites in different parts of Europe. Therefore, the performance of models at a given PSP-site was expected to be best after calibration exclusively on the two NFI-sites from the same country, as opposed to model performance after generic calibration on all NFI-sites. However, the two types of calibration led to predictions of similar integrated likelihood and NRMSE (Fig. 5-5; Fig. 5-6). It should be noted that this somewhat surprising result is partly explained by the fact that we had fewer data available per country, so the likely greater relevance of data used in within-country calibration was offset by the low weight of

evidence from using data from 2 NFI-sites as compared to 8 in generic BC. Still, it can be conjectured that the considered models are sufficiently general to provide a useful generic parameterization for Scots pine in Europe, although a future study with larger numbers of NFI-sites per country would be needed to test this hypothesis rigorously. The extra sites should be chosen to cover spatial variation in tree genotypes and geographical conditions. Such increased spatial coverage would also be needed if we want to move from assessing model predictive capacity at site-level to country-wide upscaling.

5.4.3 Quantifying and reducing uncertainties

The extent to which Bayesian calibration can reduce parameter uncertainties of a model depends both on the structure of the model and on the prior distribution assigned by the modeler. In the present study, Bayesian calibration reduced parameter and output uncertainty of all models except the parameter-richest one, ANAFORE. Likewise, the Bayesian model comparison was able to identify which models were most plausible by calculating the integrated likelihood for each model at different stages in the study. The integrated likelihood accounts for parameter uncertainty (by integrating over its distribution) and is a natural way of combining diverse measurements in one model comparison criterion. This is in contrast to the commonly used NRMSE, which has to be calculated for every variable separately. Another potential advantage of the integrated likelihood over other measures, such as NRMSE and squared correlation coefficient, r^2, is that the integrated likelihood can account for different levels of uncertainty about measurement error for different data points. However, that did not play a role in the present study because all height and diameter data were assumed to have the same degree of uncertainty.

5.4.4 Impact of the choices of prior distribution

As discussed in the sections 5.4.2 to 5.4.4, the choices made to set the prior probability distributions for the parameters of the different models affected our results to some degree, in particular in the early stages of the analysis where the prior predictive performance of the models was quantified and compared. Because prior distributions for structurally different models cannot be set in a standardized way, and were based on the expertise of the responsible modelers, this introduced a subjective element in the study. This included model-specific choices about parameter-screening, i.e. which of a model's parameters to include in the Bayesian calibration. This subjectivity concerning the prior parameter

distribution is unavoidable, to some extent, in any application of Bayesian methodology. However, the procedure we applied here, where all models were calibrated on the same data (NFI) and were subsequently compared against the same independent data (PSP) removed much of the effect of the choice of prior (Fig. 5-3; Fig. 5-4). We therefore suggest that Bayesian model comparisons are most useful after such standardization.

5.4.5 On the use of multiple models

The use of BMC is formally conditional on one of the models being 'correct' – which is never truly the case in environmental modeling – so we should use the results from the BMC as a guide towards finding the most plausible model in the set of six rather than as formal model probabilities. The results suggest that the 4C model should be recommended as the model of choice for a forest manager who wants to select a single model to help estimate future productivity out of the six models in this study. We believe that for the forest scientist the results are less clear-cut because the Bayesian probabilities do not by themselves explain what makes one model structure more plausible than another. The Bayesian model comparison largely treats the models as black boxes characterized by their input-output relationships. In a previous Bayesian forest model comparison (Van Oijen et al. 2011) it was therefore recommended that after the BC of all models, and their BMC, a detailed analysis should be carried out of the model-data mismatch remaining after calibration. It was recommended in particular to decompose likelihoods into terms for individual output variables and to decompose mean squared errors (MSEs) into terms for bias, variance mismatch and phase-shift (Kobayashi & Salam 2000). However, in our study with only two output variables and extremely short time-series, these decompositions are not informative. To allow such detailed study of model-data mismatch – and therefore to help explain the results presented here – we would need more detailed data sets, e.g. long time-series of annual data.

Another natural follow-up to BMC, and one that was carried out in this study, is calculating forecasts using Bayesian model averaging (BMA, e.g. Kass & Raftery 1995). In BMA, no single model is selected for making predictions; instead the probability distributions for the individual model predictions are averaged using as weights the model probabilities determined by the BMC. Because BMA integrates parameter and model structural uncertainty, it is less prone to underestimation of predictive uncertainty than the common practice of selecting and using only a single 'best' model. In the present study, the out-of-sample predictive capacity of BMA was very good, as shown by the NRMSE-values for both

output variables in the prior BMA. This is not exceptional; BMA has been reported to have higher forecasting skill than each individual model in other fields, such as medical prognosis (Hoeting et al. 1999) and climate prediction (Min & Hense 2006). We found that the predictive performance of posterior BMA was only average. However, this was a partly within-sample test - with model probabilities (but not parameters) informed by the PSP-data – so this should be repeated with independent data.

5.5 Conclusions

Bayesian calibration successfully reduced uncertainties in parameters and predictions of five out of six forest models. Calibrating models separately for each country did not clearly improve within-country predictive capacity compared to generic calibration. This might change when more data become available per country. Bayesian model comparison using NFI- and PSP-data identified the 4C model, which is of moderate complexity but mechanistic, as the most plausible forest model after calibration. The main caveat to the results is the issue of model initialization: how it is carried out and which data are available for it. This study suggests that models are favored that are initialized using on-site measurements of tree growth, unless model complexity requires more data for such initialization than are available. But model ranking might have been different if more data, or data from other variables than mean tree height and stem diameter, would have been available for use. For a detailed analysis of model-data mismatch, NFI-data are insufficient, but information from PSPs not used in this study, such as single tree data, could be used. BMA afforded good out-of-sample forecasts of forest productivity and may be a promising tool for forest management, of sufficient accuracy and precision whilst not underestimating uncertainties.

5.6 Acknowledgements

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6 A plant's perspective of extremes: Terrestrial plant responses to changing climatic variability[5]

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Abstract

We review observational, experimental and model results on how plants respond to extreme climatic conditions induced by changing climatic variability. Distinguishing between impacts of changing mean climatic conditions and changing climatic variability on terrestrial ecosystems is generally underrated in current studies. The goals of our review are thus (1) to identify plant processes that are vulnerable to changes in the variability of climatic variables rather than to changes in their mean, and (2) to depict/evaluate available study designs to quantify responses of plants to changing climatic variability. We find that phenology is largely affected by changing mean climate but also that impacts of climatic variability are much less studied although potentially damaging. We note that plant water relations seem to be very vulnerable to extremes driven by changes in temperature and precipitation and that heatwaves and flooding have stronger impacts on physiological processes than changing mean climate. Moreover, interacting phenological and physiological processes are likely to further complicate plant responses to changing climatic variability. Phenological and physiological processes and their interactions culminate in even more sophisticated responses to changing mean climate and climatic variability at the species and community level. Generally, observational studies are well suited to study plant responses to changing mean climate, but less suitable to gain a mechanistic understanding of plant responses to climatic variability. Experiments seem best suited to simulate extreme events. In models, temporal resolution and model structure are crucial to capture plant responses to changing climatic variability. We highlight that a combination of experimental, observational and /or modeling studies have the potential to overcome important caveats of the respective individual approaches.

Keywords: Climate change, Plant phenology, Plant physiology, Observations, Experiments, Models, Combined approaches

6.1 Introduction

Although the spatial and temporal extent of future climatic changes is still partly uncertain (IPCC 2007a), it is likely that the adaptive capacity of terrestrial plants and ecosystems will be exceeded in many regions (IPCC 2007b). Already today, responses to climate change can be observed for individual species and ecosystems (e.g. Allen & Breshears 1998; Gitlin et al. 2006) but also across species and organizational scales (e.g. Walther et al. 2002; Allen et al. 2010; Lindner et al. 2010). Climate change may manifest itself in two fundamentally different ways: in a change in the mean of for example temperature or precipitation, and in a change in their variability (i.e. variance and/or distribution, Fig. 6-1; Rummukainen 2012; Seneviratne et al. 2012). It is important to note that these terms relate to steady-state systems. The climate system and ecosystems however are in permanent transition and therefore the term 'mean' and 'variability' only make sense relative to well-defined spatial and temporal scales. Moreover, mean and variability may not be fully independent (e.g. an increasing mean value often implies increasing standard errors). Here, we still treat changes in mean and variability as two separate aspects, defining changes in the mean as changes over longer time periods (e.g. inter-annual changes) and changes in variability as changes over medium/short term periods (e.g. inter-daily changes) of climatic variables. We define extreme events from this climatological perspective as increasing climatic variability (i.e. increasing variance and/or changing distribution) in contrast to changes in mean climate. Our aim is to emphasize the generally unrecognized distinction between impacts of changing mean climate and changing climatic variability on terrestrial ecosystems.

We center but do not limit our synthesis on a plant's perspective of temperature and precipitation extremes, since these are the most important climatic determinants of plant growth and survival globally (e.g. Boisvenue & Running 2006). Observations since 1950 show that the length of warm spells and heat waves increased (e.g. Barriopedro et al. 2011; Rahmstorf & Coumou 2011; Seneviratne et al. 2012). More intense and longer droughts are observed but at the same time the number of heavy precipitation events increased (Seneviratne et al. 2012 and references therein). Future projections on changes in climatic variability show strong spatial and temporal heterogeneity (Giorgi et al. 2004; Orlowsky & Seneviratne 2012) and are highly uncertain (Seneviratne et al. 2012). Using multi-model experiments, Barriopedro et al. (2011) for instance found that the probability of summer heatwaves may increase by a factor of 5-10 in the future while Schär et al. (2004) predict that temperature variability will increase by a factor of 2 in Europe. Projected changes in extreme precipitation events (droughts or flooding) are even more uncertain. Orlowsky & Seneviratne 2011

derived from their simulations with an ensemble of general circulation models (GCMs) robust projections on increasing droughts over the Mediterranean and increasing heavy precipitation over the Northern high latitudes.

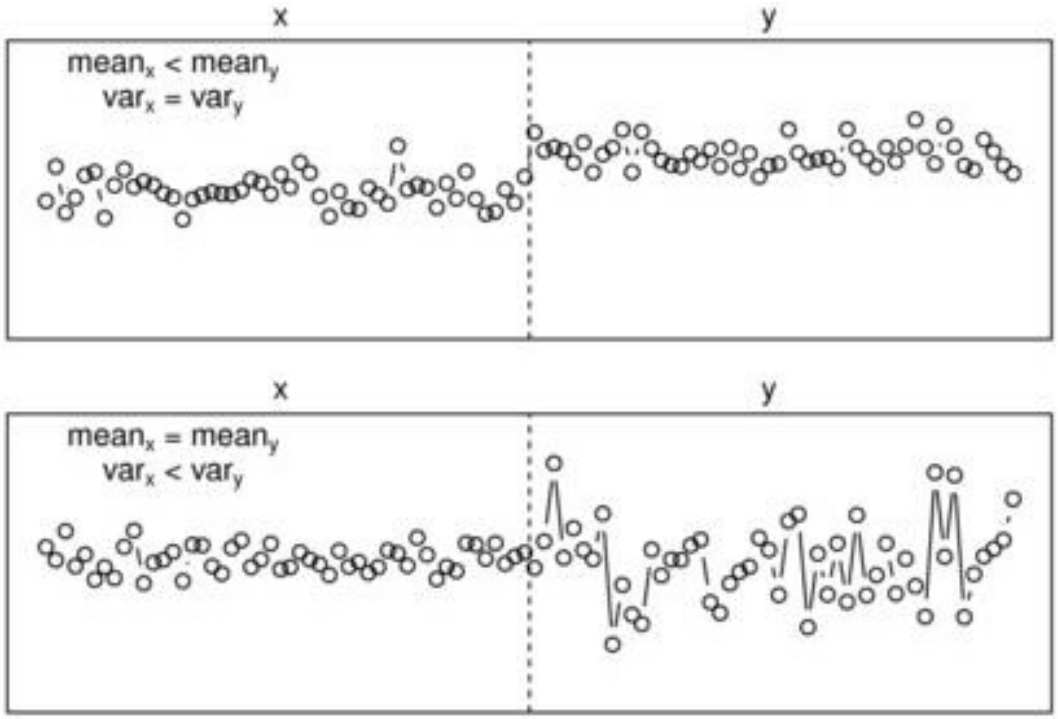

Fig. 6-1 The two theoretical cases of changing climatic drivers: (1) changes in the mean but not the variance (upper panel), (2) changes in the variance but not the mean of a variable (lower panel). A third case is conceivable where both the variance and the mean remain comparable, but rare, very extreme events occur, changing essentially the nature of the distribution. Importantly, any discussion of means vs. extremes requires a temporal reference, as a short-term increase in the mean may turn out to be a long-term increase in the variance.

While changes in the mean values are important, there is evidence that plant distribution (Chapin et al. 1993; Bokhorst et al. 2007), survival (van Peer et al. 2004) or net primary productivity and species diversity (Knapp et al. 2002) respond to extreme rather than to average conditions (Jentsch & Beierkuhnlein 2008). Additionally to that, different physiological processes such as photosynthesis, water relations or nutrient uptake at the species, community or ecosystem level affect the response of plants to climatic variability (Fig. 6-2). To account, for example, for changing precipitation distributions, Knapp et al. (2002) decreased precipitation frequency but not its total amount in a mesic grassland leading to more intense precipitation events. They found reduced carbon turnover but increased species diversity. Drier conditions also tend to decrease evapotranspiration, which leads to lower evaporative cooling (Teuling et al. 2010). In combination, warming and drought can

therefore lead to additional warming of an ecosystem (Seneviratne et al. 2006; Fischer et al. 2007; Kuster et al. 2012).

In addition to the impacts of changing climatic variability, the physiological response of terrestrial plants depends also on interactions between species (Thorpe et al. 2011) and their ability to adapt and acclimate. The water available for plants depends on the water holding capacity of the soil (Kramer & Boyer 1995; Porporato et al. 2004; Leuzinger & Körner 2010; Raz-Yaseef et al. 2010), competition with other plants (Casper & Jackson 1997) and precipitation patterns (Knapp et al. 2008). The latter has different effects on soils with high or low water holding capacity (i.e. a stronger or weaker buffer against drought; Knapp et al. 2008) or on flood occurrence, which is an important driver of plant distribution (Crawford 1992; Colmer & Flowers 2008; Parolin & Wittmann 2010). Furthermore, interactions between changing climatic variables as well as thereby induced community shifts may affect the response of plants to new conditions (Langley & Megonigal 2010; de Boeck et al. 2011). For example, a drier and warmer climate will exert stronger constraints on plant growth than a warmer but also wetter climate; or rising CO_2 may alleviate the impact of drought (Morgan et al. 2004; Holtum & Winter 2010). Moreover, more prolonged dry periods will alternate with more intensive rainfall events, both within and between years, which will change soil moisture dynamics (Weltzin et al. 2003; Porporato et al. 2004; Fay et al. 2008; Knapp et al. 2008; Bartholomeus et al. 2011a). Eventually, it is also crucial how quickly plant communities adapt genetically to the imposed changes. The IPCC (2007b) concluded that the rate of natural adaptation will be slower than the rate of climate change. Natural adaptation differs between species: while species with short generation times may adapt within years, Rehfeldt et al. (2001) for example estimate that it will take 2-12 generations (an equivalent of 200-1200 years) for a coniferous trees species to show genetic adaptation in response to climatic change. All these factors determine whether plants at a specific site will experience changing climatic variability as extreme or not.

Thus, the vulnerability of terrestrial plants to climate change will, besides changes in the mean, largely depend on the changes in the climatic variability and the occurrence of extreme events. The understanding of this difference in experiments and model simulations requires very good knowledge of the baseline or control climate (especially the background variability to which plants are adapted to). This complies with the fact that extreme conditions per se have shaped ecosystems for a long time (Körner 1998, 2003) and may also foster adaptation and thus decrease sensitivity (Hegerl et al. 2011). A plant's response to specific environmental conditions produces its specialized set of traits which allows it to prevail over competitors and occupy a specific habitat (Körner 1998,

2003). We use the term 'stress' throughout this review according to Lortie et al. (2004) to refer to situations in which plants experience critical environmental conditions beyond what they experience normally (Chapin 1991) such that damage to vital function occurs (see Gaspar et al. 2002).

In this paper we strive to answer the following questions:

- Which plant processes are vulnerable to changes in the variability of climatic drivers rather than to changes in their mean?
- How can we quantify responses of plants to changing climatic variability?

We present evidence from experiments, observations and modeling studies that help to understand the current and future responses of individuals and communities to changing variability, with a particular focus on temporal and spatial patterns. These examples also help to identify important research gaps. We do not aim to cover the literature on these topics systematically.

6.2 Which plant processes are vulnerable to changes in the variability of climatic drivers rather than to changes in their mean?

The vulnerability of plants refers to their susceptibility to adverse effects of environmental change (IPCC 2007b). Estimates of vulnerability depend on the definitions (e.g. the definition of death (Zeppel et al. 2011)) and the spatiotemporal scale considered. The ultimate limit to withstanding environmental stress from an individual plant's perspective is mortality due to physiological failure ("You can only die once") but at the community level, already reductions in growth and subsequently competitiveness may constitute a limit to species fitness. For commercial crops it may even be a critical reduction in productivity so that cultivation is discontinued.

In the following sections, we discuss the vulnerability of phenological and (individual and interacting) physiological processes to changes in the climatic variability rather than the mean of climatic drivers and we highlight how these play out at the species and the community level (see schematic overview in Fig. 6-2). Our list of examples is not exhaustive but meant to illustrate this important difference between changes in climatic variability rather than the mean.

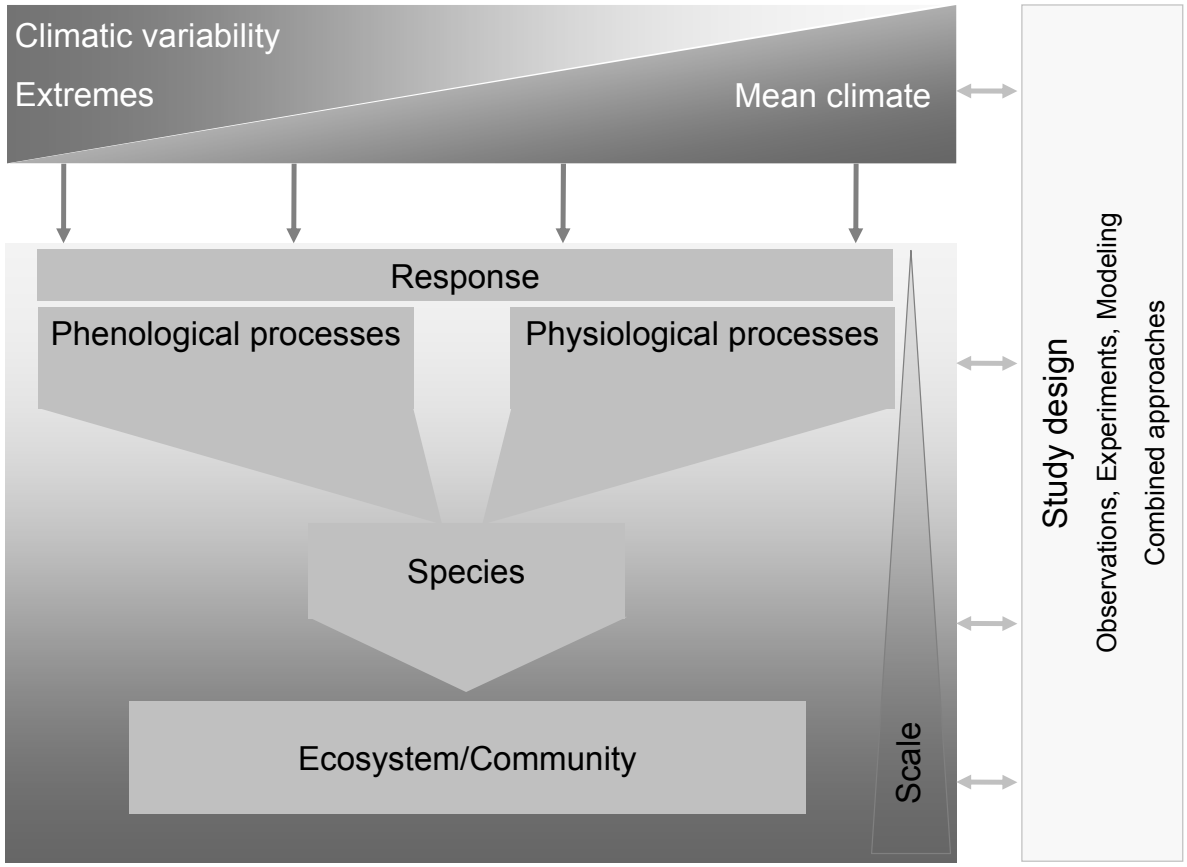

Fig. 6-2 Conceptual overview of the different processes and scales affected by extremes and the study designs to assess them.

6.2.1 Phenological processes

One of the well-studied responses of plant species or communities to environmental change is phenology, which tracks seasonal events in generative and vegetative plant growth. Given the predominant influence of climate (with the important exception of photoperiodism, see Körner & Basler 2010), phenology has emerged as a key tool in identifying fingerprints of anthropogenic climate change in nature (Menzel et al. 2006). Observed large-scale phenological changes such as an earlier onset of leaf unfolding/ flowering (Menzel & Fabian 1999; Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003; Menzel et al. 2006) are mainly driven by changes in mean climatic conditions especially temperature (Vitasse et al. 2009; Polgar & Primack 2011; see also Table 6-1).

Phenological changes in response to changing climatic variability are much less studied although they clearly interact with phenological changes induced by changing mean climate. For example, in the temperate and boreal zones which are often temperature limited, a central trade-off revolves around maximizing the vegetation period while avoiding frost damage (Kramer et al. 2010). An

untimely response to early warm spells may be fatal but can bring enormous advantages for early successional or opportunistic species (r-strategists, Leuzinger et al. 2011a). In contrast, long-lived, late successional species often have chilling requirements and photoperiodic safety mechanisms (Heide 1993) and thus may be in a position to avoid increasing risks of late frost due to changing climatic variability but would also benefit less from early warm spells. This is supported by the fact that the risk of damage due to late frost events has not increased so far for several coniferous and broad-leaved species in Central Europe (Scheifinger et al. 2003; Menzel et al. 2003). Besides this example, there is further evidence, that extreme events may alter phenological responses depending on their timing and strength (e.g. Jentsch et al. 2009; Menzel et al. 2011). This can lead to unexpected effects such as second flowering in autumn or extended flowering until the beginning of winter for some species (Luterbacher et al. 2007). Moreover, extreme warm spells decreased the differences in spring phenology between urban and rural sites (Jochner et al. 2011). Furthermore, only half of the trees reached leaf maturity in an extreme drought experiment in the Mediterranean (Misson et al. 2011). Overall, the response of phenology to climatic variability seems to be less well understood than to changing mean climate although increasing climatic variability may have a strong damaging potential.

Table 6-1 Examples of observed plant vulnerabilities to changes in the mean climate and climate variability.

Process	Changing mean	Effect/Response	Reference	Changing variability	Effect/Response	Reference
Phenology	Increase in mean temperature	Prolongation of growing season, earlier onset of leaf unfolding and first flowering, delay of leaf senescence	Menzel & Fabian 1999; Walther et al. 2002; Parmesan & Yohe 2003; Root et al. 2003; Menzel et al. 2006; Polgar & Primack 2011; Vitasse et al. 2009	Early and late frosts, warm spells, drought, heavy rain	Frost damage, possibly fatal damage to opportunistic species, second or extended flowering, advanced mid-flowering, decreased flowering length	Leuzinger et al. 2011a; Luterbacher et al. 2007; Jentsch et al. 2009
Soil organic matter decomposition	Increase in mean temperature	Potentially increase in soil organic matter decomposition	Saxe et al. 2001	Droughts/heatwaves	Increase in soil water repellency leads to reduced decomposition of soil organic matter	Goebel et al. 2011
Water relations	Increase in night-time warming (and mean temperature)	Slight increases in stomatal conductance	Albert et al. 2011	Drought	Stomatal closure and carbon starvation (isohydric plants), hydraulic failure (anisohydric plants)	Breda et al. 2006; McDowell et al. 2008

6.2.2 Physiological processes

We here focus on the response of plant water relations such as transpiration to climatic variability (drought/heat waves and excess water). Increasing temperatures and/or heat waves combined with less precipitation or more variable precipitation events lead to prolonged dry periods and high atmospheric demand for plant transpiration, which determine drought stress of plants beyond changes in mean climate (Schimper 1903; Porporato et al. 2004). Barriopedro et al. (2011) predict such an increase in drought events for the 21st century and the consequences for plant water relations are well documented (e.g. Leuzinger et al. 2005; Bréda et al. 2006; Granier et al. 2007) although not all mechanism are fully understood. There is an ongoing debate about two competing response strategies to drought: Isohydric plants may respond by closing their stomates thus reducing their water loss but eventually facing carbon starvation, whereas anisohydric plants keep their stomates open thus running the risk of hydraulic failure (Mc Dowell et al. 2008; Sala et al. 2010; Zeppel et al. 2011). Furthermore, Craine et al. (2012) highlighted the importance of the timing of an extreme event for grassland productivity. The response of plants to drought is of such an importance that Hartmann (2011) refers to it as a "change of evolutionary forces" from competition for light to competition for water and carbon. The responses of plants to climatic variability and particularly drought have important consequences for net primary productivity (NPP) and hence carbon cycling even at large spatial scales such as Europe (Ciais et al. 2005; Dury et al. 2011). Thus, plant responses to increasing drought events and heat waves influence plant functioning across spatial and temporal scales.

Also climatic variability resulting in excess water (i.e. flooding or waterlogging), can induce important physiological responses by terrestrial plants. Due to waterlogging, O_2 diffusion and supply to the roots is reduced, and the oxygen demand of plant roots, (i.e. root respiration – oxygen consumption in the roots), cannot be fulfilled (Lloyd & Taylor 1994; Blom & Voesenek 1996; Kozlowski 1997; Amthor 2000). This results in waterlogging/ oxygen stress, i.e. lack of oxygen due to high soil moisture contents (Bartholomeus et al. 2008). Both the oxygen supply and demand may be affected by a more extreme climate, due to more intense precipitation and higher temperatures (respiration increases with temperature), respectively. Therefore, to analyze the effects of low soil oxygen availability on species performance, it is necessary to integrate the soil physical and plant physiological processes, thus accounting for both the oxygen supply to and oxygen demand of plant roots (Bartholomeus et al. 2011b). Besides reduced root respiration rates, the decrease of water absorption due to waterlogging stress causes sensitive plants to wilt in a similar way to drought

(Jackson & Drew 1984). Many species already growing in flood-prone habitats have developed different strategies to survive hypoxia, by producing aerenchyma and/or adventitious roots in response to an increase in the concentration of ethylene and auxin (Blom & Voesenek 1996). Flooding can also give rise to detrimental effects at leaf level, by inducing stomatal closure and, consequently, limiting gas exchange and plant growth (Kramer 1951; Chen et al. 2005; Rengifo et al. 2005; Fernandez 2006). Thus, similarly to drought, extremes of excess water, in combination with higher temperatures, strongly alter plant physiological processes such as carbon uptake and transpiration.

In conclusion, we note that plant water relations seem to be very vulnerable to increasing variability in temperature and precipitation and that changing heatwaves and flooding have stronger impacts on physiological processes than changing mean climate (see also Table 6-1).

6.2.3 Interacting physiological processes

The interaction of physiological processes such as photosynthesis, nutrient uptake and water relations may strongly affect the response of plants to changing climatic variability. Furthermore, interactions among several global change drivers or between global change drivers and other environmental variables, may result in other growth-limiting factors (e.g. soil type) becoming less important. Drought periods, for example, may have the potential to not only determine growth or mortality in an ecosystem but also to cause shifts in growth-limiting factors such as nutrient limitations. For example, in an experiment of Kuster et al. (2012) oaks were grown on two different soil types with different nutrient availabilities. Under well-watered conditions, growth on one soil was lower due to nutrient-limiting conditions, whereas under repeated drought periods these differences disappeared. This shows that growth-limiting factors such as nutrient availability can become less important under changing climatic variability, while they may be overlooked if only changes in mean climate are considered. There are many other examples of interacting processes under changing climatic variability such as ozone stress during periods of high temperature (Matyssek et al. 2010; Pretzsch & Dieler 2011).

The interactions of physiological processes can however be even more intriguing. In coastal habitats (i.e. the interface of terrestrial and aquatic habitats) which are not only saline, but are also prone to flooding (e.g. mangroves and salt marshes) (Colmer & Flowers 2008) *Tamarix africana* Poiret, for example, showed a reduction of CO_2 assimilation rates only in young *Tamarix africana* Poiret leaves after 45 days under continuous flooding with saline water (200mM), while old leaves and the

aboveground relative growth rate were not affected by the treatment (Abou Jaoudé et al. 2012). Thus, while parts of the plants actually responded to flooding, this was not the case for the entire plant. This example is rather related to changes in mean climatic conditions (i.e. temperature-induced rising sea levels) but it highlights that changing climatic variability is likely to interact with an already complex interplay of physiological processes.

6.2.4 Species-level processes

At the species level, responses of different genotypes to climate provide information how a species may react to changing climatic variability. Since genotypic variation results in different sensitivity thresholds of distinct ecotypes to changing climatic variability it can partly substitute lacking data of changing climatic variability for a specific genotype. In an ecotype study (Klein et al. submitted) that included all three climate types (meso-Mediterranean (MM), thermo-Mediterranean (TM), and semi-arid (SA) within the natural distribution of the forest tree *Pinus halepensis* Mill. (and hence three very different combinations of mean climate and climate variability), two major physiological adjustments were identified: (1) shortening of the growing season length (from 165 to 100 days) to match a shorter rainy season and (2) increasing water use efficiency (from 80, to 95, to 110µmol CO_2 mol^{-1} H_2O under MM, TM, and SA climates respectively). However the sensitivity threshold differed in between ecotypes: Northern ecotypes mainly responded to the change MM to TM, whereas Southern ecotypes responded to the change TM to SA. At the species level, the study showed that higher xylem sensitivity to embolism in specific ecotypes matched previous reports (Atzmon et al. 2004; Schiller & Atzmon 2009) of significantly higher mortality rates in these ecotypes under yet harsher conditions. These observations suggest that while hydraulic constraints in response to climatic variability limited the distribution of a tree species, plasticity in water use efficiency and growth phenology enabled its success under a wide range of climatic conditions.

6.2.5 Community-level processes

At the community level, phenological, physiological and species-level processes as well as their interaction culminate in complex responses to changing mean climate and climatic variability (Fig. 6-2). Species range shifts have been associated with changes in mean climate (Lenoir et al. 2008; Harsch et al. 2009) but also with changing climatic variability (Kelly & Goulden 2008; Doak & Morris 2010). They lead to a disruption of ecological communities and species interactions due to different dispersal speed and success. These processes differ between the trailing and the leading edge of a

population (Kramer et al. 2010; Doak & Morris 2010). From a community's perspective such range shifts may entail positive (e.g. release from competition) and negative (e.g. loss of important pollinator) consequences. Despite these important consequences of range shifts, it is yet unclear whether changing mean climate or changing climatic variability will be the more important driver of range shifts.

At the community level, for annual plants, the variability of rainfall is important for the success of germination. Increasing climate variability can have both negative and positive effects on species persistence and thus plant population dynamics (Levine et al. 2008). Climatic fluctuations, for example, may enable species to avoid interspecific competition if species differ in the years in which they perform (e.g. reproduce or grow) best (Levine & Rees 2004). Dormancy and germination biology determine whether temporal variability favors or inhibits species persistence (Levine & Rees 2004) and can thus be limiting for a species (Godefroid et al. 2011). Temporal variation in resource availability as induced by climatic variability may reduce the effects of competitive exclusion, allowing more species to coexist (Knapp et al. 2002).

A combination of extremes/multiple stresses may not only hamper performance but may also drive extinctions (Smith & Huston 1989; Niinemets & Valladares 2006). As functional trade-offs exist in adjusting to multiple environmental limitations (Holmgren et al. 1997; Silvertown et al. 1999), adapting to one stressor may go at the cost of adapting to another (Holmgren et al. 1997; Niinemets & Valladares 2006). This trade-off among the tolerances to multiple environmental limitations hampers niche differentiation (Niinemets & Valladares 2006). Bartholomeus et al. (2011a) demonstrated that the interaction between both the wet and dry extremes of plant water stress (oxygen/waterlogging and drought stress) is particularly detrimental to the survival of specialists and of endangered plant species. Both wet and dry weather extremes may increase due to changing climatic variability, thus increasing the risk of a combination of these stressors to occur at a site (Knapp et al. 2008; Bartholomeus et al. 2011a). This may favor generalists over specialists and rare species and thus influence vegetation dynamics and associated ecosystem services in response to changing climatic variability at the community level.

6.3 How can we quantify responses of plants to changing climatic variability?

Just as responses to global change in general (Rustad 2008), the responses of plants to changing climatic variability can be assessed in observational, experimental and modeling studies and

combinations of these approaches (Fig. 6-2). All these approaches have their limitations in assessing a plant's perspectives of extremes: on the one hand, observational studies are by definition 'opportunistic' in the sense that extreme conditions such as a long-lasting drought can not be planned (Smith 2011). On the other hand, scaling and higher-order interactions are an important issue in experimental and modeling studies (Leuzinger et al. 2011b; Wolkovich et al. 2012). Furthermore, it is crucial for any type of study that claims to assess climate variability to report whether changing mean climate and/or changing climatic variability have truly been measured and what the background variability of the system is over a well-defined time period. We qualitatively show this in Table 6-2 for a number of studies cited above as a first attempt to foster consistent reporting of studies dealing with climatic variability.

Table 6-2 Are we measuring the impact of mean climate or climate variability? Non-exhaustive list of the studies cited in the text and their testing amplitude in comparison to the background variability of the respective study system. The last column indicates in a qualitative way how well the testing amplitude accounts for climatic variability in terms of the background variability.

Study system	Testing amplitude	Background variability	Study type	Reference	Testing climate variability?
European grassland & heath species	Drought: 32 days	Local 100-year extreme drought (number of days with precipitation < 1mm), 33 days of drought in 1976	Experiment	Jentsch et al. 2009	Yes, 100-year-event
European grassland & heath species	Precipitation: 170mm over 14 days	Local 100-year rainfall extreme, 152mm of precipitation over 14 days in 1977	Experiment	Jentsch et al. 2009	Yes, 100-year-event
European plant phenology	+1.5 (warm), +3 (very warm), −1.5 (cold) and −3 (very cold) standard deviations from the long-term mean at the respective grid point to classify warm and cold spells	Long-term mean	Observation	Menzel et al. 2011	Yes, +/- 3 standard deviations from mean
Grasslands	6-8 large precipitation events per growing season (mean per event = 42 mm)	The size and frequency of precipitation events in the treatment are within the documented range of precipitation regimes of the past 100 years.	Experiment	Knapp et al. 2002	Yes, but less than 100-year-event
Young oak stands (3 species (*Quercus robur, Quercus petraea, Quercus pubescens*), 4 provenances each)	Amount of irrigation water in drought-treated stands was 60% lower than the long-term mean precipitation (728 mm during the growing season from April to October) in 2007 and 43% lower in 2008 and 2009. Experimental droughts were imposed by stopping irrigation for several consecutive weeks during selected periods in the growing season.	In comparison to the long-term mean of the site, irrigation in the control was 16% lower in 2007, 26% higher in 2008 and 30% higher in 2009.	Experiment	Kuster et al. 2012	Unclear but testing amplitude much larger than variability in control
Mixed broadleaved forest in Central Europe	Seasonal precipitation: 50% of the 10-year mean from 1989 to 1999, Spring precipitation: below the mean, Mean monthly temperatures: exceeded the 10-year mean from 1989 to 1999)(e.g. + 6.8 °C for June).	Long-term mean	Observation	Leuzinger et al. 2005	Unclear (background variability not further specified) but likely
Pinus halepensis stands (3 contrasting sites, 5 provenances)	Precipitation in Rome, 766+-156mm; Tel Aviv, 557+-184mm, and Yatir (semi-arid), 279+-88mm	Long-term mean (differences in mean climate are very large hence testing amplitude equals high background variability but no explicit testing of climate variability)	Transplantation	Klein et al. submitted	Locally unclear but over the species distribution range probably yes
Tamarix africana Poiret	Continuous soil flooding with fresh and saline water during 45 days.	Not explicitly mentioned, plants survived 45 days of flooding	Experiment	Abou-Jaoudé et al. 2012	Unclear

6.3.1 Observational studies

Observational studies elucidate a plant's perspectives of extremes, if by chance they cover extremes. This makes them inherently opportunistic (Smith 2011) unless they involve some retrospective elements such as dendrochronology. Observations from 'extreme' (from a plant's perspective) sites (e.g. from the leading and trailing edge of a population (Doak & Morris 2010)) can help us learning about the limits and coping range of plants. To this end, GIS mapping of 'extreme' sites within a species' distribution requires careful interpolation of weather/climate data collected at appropriately distributed climate stations. However, 'extreme' sites are sometimes only poorly studied since they represent marginal ecosystems, whose services are not fully valued by society and have thus been outside the main focus of researchers. The psamophilic plants and vegetation of the beaches and dunes of the Portuguese coast, for example, are highly adapted to very specific environmental conditions and directly exposed to sea level rise, storms and severe erosion processes. Unless their ecological requirements, functioning as communities and most influential physical drivers are understood, it will be difficult to study their responses to future climate change (Martins et al. accepted). It is however important to note, that in some disciplines there is a strong focus on extreme sites (such as on cold, high elevation or very dry sites in dendrochronological studies (e.g. Gruber et al. 2012)) which in turn may complicate studying mean climate impacts.

Generally, observational studies are well suited to study plant responses to changing mean climate, since long-term ecological data can be matched with increasingly available climatic observations. They are less suitable to gain a mechanistic understanding of plant responses to climatic variability since usually too many factors are involved and not all are measured.

6.3.2 Experimental studies

Experiments allow for controlled conditions and factorial experiments in the field and laboratory, have a long history in ecological research and are of crucial importance for global change studies (Luo et al. 2011)). When quantifying climate change impacts however, field experiments can usually only test a limited number of factors and their combinations due to financial and logistic constraints (Templer & Reinmann 2011). Therefore, interactions can often not be fully assessed (e.g. Wolkovich et al. 2012). Furthermore, to provide answers to the question of how extreme climatic events impact on ecosystems, experimenters should ensure that the applied treatment is indeed 'extreme' beyond the current background

variability of the system over a well-defined time period, running the risk of killing plants (Leuzinger & Thomas 2011; Beier et al. 2012).

Also, the temporal scale influences the outcome of an experiment. A comparable set of factors and a minimal experimental duration, for example, for all drought experiments would therefore be desirable. However, even then, most experiments would have to stop after few years. This raises the question whether the experiment actually simulates extreme situations or long-term change and whether the system recovers after the experiment ends. The high diversity in the response of growth parameters of oaks to drought as discussed in Kuster et al. (2012), shows that in experimental conditions, e.g. treatment duration and intensity, tree age or experimental set up, have to be considered in the evaluation of drought effects on trees. Thus it is crucial to assess what degree of change and what temporal scale experiments cover if we want to evaluate whether they actually simulate responses to changing climatic variability, or rather to changing mean climate.

In a transplantation study, for example, the effect of a drying and warming trend was obtained by comparing tree performance in Rome (Italy), Tel Aviv (Israel) and Yatir (Israel) along a precipitation gradient (Klein et al. submitted). The sites differed significantly in their mean annual precipitation, each representing a different climate type, but the responses were interpreted as drought acclimation. Results from this study captured many plant adjustments that were induced by both phenotypic plasticity and locally adapted ecotypes. Such transplantation experiments along altitudinal or latitudinal gradients do not require manipulation of the environment and may be an alternative to laboratory/greenhouse experiments. So far, transplantation experiments have not been considered in comparative studies of different artificial warming methods (e.g. Aronson & McNulty 2009). However, such experiments seem to be well adapted especially for long term experiments, as they project a realistic simulation of future climate conditions considering also the length of the growing period, one of the most important limiting factors in alpine plant growth (Jonas et al. 2008). Similar to laboratory/greenhouse experiments it is crucial that the results are interpreted in terms of changing mean climate and changing variability over well-defined temporal scales.

6.3.3 Modeling

Models can be used as diagnostic and predictive tools that integrate results from experiments and observation to gain mechanistic understanding and allow testing hypotheses generated from field data, experiments and theory (Leuzinger & Thomas 2011;

Luo et al. 2011). Models have to be designed for a specific purpose and here we discuss which are suitable to simulate plant responses to changing climate variability. This is a highly relevant question, since models that account for extremes may require a different structure, for example an appropriate time resolution, to capture an extreme precipitation event. Many forest models for example use monthly input data and are thus unable to account for short-term extreme events (e.g. Bugmann 2001). Forcing such a model with daily weather instead with monthly climate data improved its performance (Stratton et al. 2012). Zimmermann et al. (2009) argue that for capturing some ecosystem responses even daily climate data may be insufficient since they smooth meteorological extremes.

Generally, effects of climate change on ecosystems are analyzed by driving simulation models with output from GCMs and regional climate models (RCMs). To account for the uncertainty of climate change projections, besides different scenarios, also several GCMs (e.g. Buisson et al. 2010) and different realizations of a scenario may be used. Many models do not use the original GCM/RCM data at hourly resolution (which may also not always be available) but only daily or monthly aggregations and thus strictly speaking miss some of the meteorological variability. The CARAIB dynamic vegetation model (Otto et al. 2002; Laurent et al. 2008; Dury et al. 2011), for example, derives daily values of meteorological variables, as usual in large-scale simulations, from monthly mean outputs from GCM/RCMs using a stochastic weather generator (Hubert et al. 1998). The sequences of daily temperature or precipitation produced by the stochastic generator are renormalized to the monthly values generated by the RCMs. Thus the precise day-to-day sequence of an extreme event in the model, such as a drought period or a succession of heat wave days (Beniston et al. 2007; Déqué 2007), depends on the distribution functions used in the stochastic generator, although the monthly values of the climate model are not altered. While evidently it is challenging for such large scale modeling efforts to integrate high-frequency climate variability, these studies are necessary to assess different feedbacks of vegetation types (e.g. feedbacks of ecosystem response to drying on near-surface temperature differ between forest and grassland ecosystems (Teuling et al. 2010) at the global scale).

Also, species distribution models face the challenge of including changing climate variability. Usually, they use information on species distribution (both potential from expert knowledge or forest communities, and actual from inventories and landcover-data) together with climate data to construct bioclimatic ranges (also called climate envelopes). They show a two dimensional frequency distribution of for example temperature and precipitation, indicating the mean climatic range, in which the analyzed species (potentially) exist. Extrapolation of

this information allows identifying regions with comparable climate to, for example, estimate a (extended) potentially occupied habitat (Guisan & Zimmermann 2000) or new growing areas outside the recent (actual or potential) distribution (Miller et al. 2004; Peters & Herrick 2004). Also the match of actual and future suitable ranges can be identified, classifying species into tolerant or intolerant to expected climatic conditions (Dunk et al. 2004; Gibson et al. 2004). This provides further understanding about expanding or shrinking habitats under changing climate (Erasmus et al. 2002; Midgley et al. 2006). Usually, climate envelopes are derived from mean values (e.g. mean temperature) and are thus designed to assess impacts of changes in mean climate. Consequently especially regions at the edge of the distribution range may appear suitable, but in reality maximum or minimum precipitation or temperature may determine the distribution range (or other, non-climatic factors such as soil type or herbivory). This can partly be circumvented by including standard deviations as variables (Zimmermann et al. 2009), and species distribution models could also be built with extremes (e.g. maximum temperature or minimum precipitation) to enhance the predictive power. Zimmermann et al. (2009) for example found that incorporating climatic extremes slightly improved models of species range limits, since it corrected local over- and underprediction, but they also argue that climate variability rather complements the response to mean climate. Thus including climate variability is one uncertainty of species distribution models that has to be considered to assess compliance of climate envelopes (Gloning et al. in prep.).

Although generally process-based modeling is required to derive climate-robust relationships to predict vegetation characteristics (Franklin 1995; Guisan & Zimmermann 2000; Schwalm & Ek 2001; Botkin et al. 2007; Suding et al. 2008; Hajar et al. 2010), this is even more evident when considering changing climate variability. Bartholomeus et al. (2011b) demonstrated that, in contrast to process-based relationships between site factors and vegetation characteristics, relations based on indirect site factors produce systematic prediction errors when applied outside their calibration rate, and so cannot be used for climate projections. Mean groundwater level, for example, is only an indirect site factor related to plant performance, as it is the interaction between soil-water-plant-atmosphere that essentially determines if plants suffer from drought stress or oxygen/waterlogging stress. When, for example, soil moisture availability is too low to meet the water demand for transpiration, a plant suffers from drought stress (Schimper 1903; Reddy et al. 2004). This so-called physiological drought (Schimper 1903), implies that not only water availability but also vegetation's demand for water has to be considered. Instead, more process-based

explanatory variables are needed to predict the effects of changing climate variability on the species composition of the vegetation. These explanatory variables should consider the interacting meteorological, soil physical, microbial, and plant physiological processes in the soil-plant-atmosphere system. Bartholomeus et al. (2011a) did so for water related stressors, by simulating respiration reduction (reflecting the combined effect of high temperature and low oxygen availability), and transpiration reduction (reflecting the combined effect of high atmospheric water demand and low water availability) for a reference vegetation. The simulated stress for reference vegetation acts as a habitat characteristic, i.e. a measure for the moisture regime of the soil to which the actual vegetation will adapt. The use of reference vegetation improves the applicability of models in which stress measures are implemented, especially in predicting climate change effects (Dyer 2009).

6.3.4 Combined approaches

Combined approaches unite experimental, observational and/or modeling studies. A recent meta-analysis shows that the temperature sensitivity of phenology in warming experiments is underestimated in comparison to observations (Wolkovich et al. 2012). It highlights that observational studies are crucial to test whether experimental results match observations in natural systems. A combination of laboratory and field studies is necessary to determine whether thresholds detected in the laboratory, are also likely to occur in the field. This is especially relevant when calculating the effects of changing climatic variability. We take leaf gas exchange and ecosystem flux measurement data from Brilli et al. (2011) as an example of how to link experiments and observation at different scales and how an experiment can complement observations to study plant responses to climate variability. Fig. 6-3 shows that evapotranspiration measured in the field with the eddy covariance method, was insensitive to soil drying over the range of soil water contents occurring in the field. The leaf gas exchange measurements during the laboratory drought experiment when extended to much drier conditions showed that the plant species occurring at this site start to down-regulate stomatal conductance at soil water contents close to the wilting point – conditions that have never been reached in the field during the observational period of 2001-2009. Back-of-the-envelope calculations suggest that ca. 10 additional rain-free days would have been required even during the 2003 and 2006 droughts in order for plants at this site to experience gas exchange limitations. Such information is crucial to assess whether responses to changing mean climate or to changing climate variability are measured.

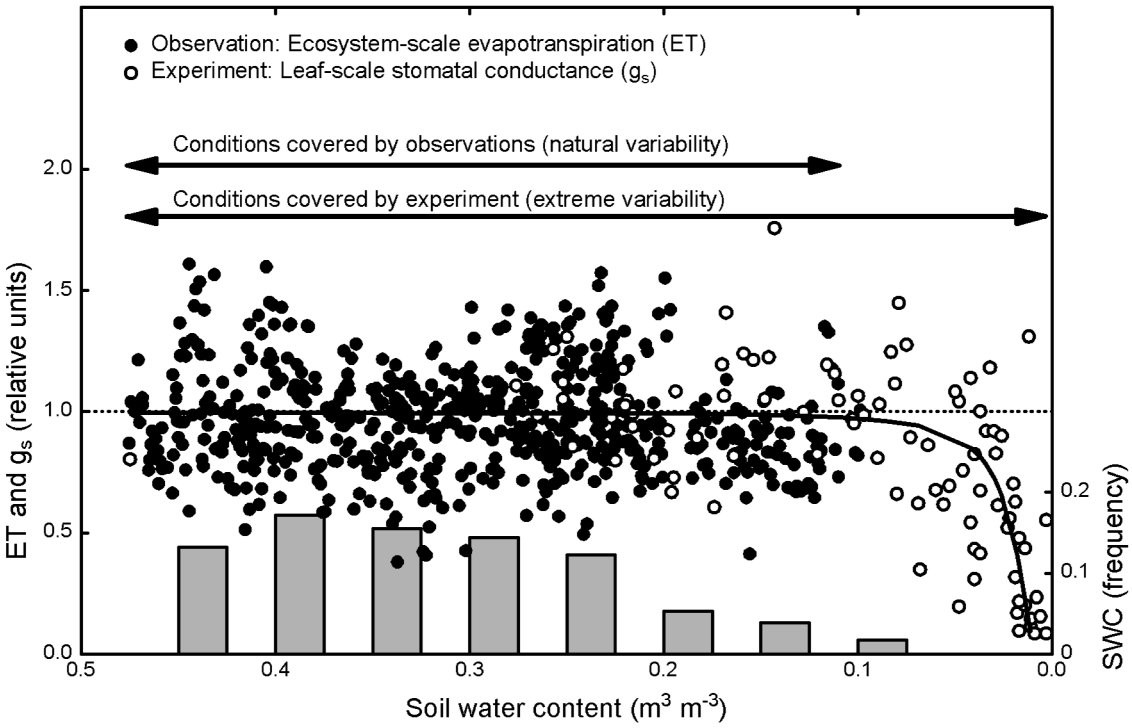

Fig. 6-3 Evapotranspiration measured in the field with the eddy covariance method (black filled dots) over the range of soil water contents (grey bars) occurring in the field and stomatal conductance measured in a laboratory experiment (black open dots). Data and further descriptions are available in Brilli et al. (2011). SWC = Soil Water Content.

Moreover results can be extended to a larger spatial scale, by combining simulation models with research tools like raster GIS (Minacapilli et al. 2009; Bonfante et al. 2011) and Digital Elevation Model (DEM) derived analysis (MacMillan et al. 2000). Furthermore, studies that combine observational or experimental results - at field scale - with simulation models of hydro-thermal regime - at landscape scale - allow to quantify the effects of changing climate variability (Bonfante et al. 2010). Riccardi et al. (2011) assessed the adaptive capacity of olive cultivars to future climate by means of a data base of cultivars' climatic requirements, combined with a spatially distributed model of the soil–plant–atmosphere system. They set up a database on climatic requirements and defined critical environmental conditions using two quantitative indicators of soil water availability (the relative evapotranspiration deficit, i.e. the ratio of actual to maximum evapotranspiration of the crop, and the relative soil water deficit, i.e. the ratio between the actual and the maximum volume of soil water available to plants taking into account the water retention characteristics, to get a comparable indicator across soil types). The response in terms of yield of several olive cultivars to these indicators was determined through the re-analysis of experimental data derived from scientific literature (Moriana et al. 2003; Tognetti et al. 2006). This database on cultivars' requirements was used in combination with a plant-soil-atmosphere model (SWAP,

van Dam et al. 2008). The model was used to describe the soil water regime at landscape scale under future climate scenarios from statistically down-scaled GCMs, resulting in several realizations (Tomozeiu et al. 2007). The indicators of soil water availability were thus determined in different soil units, and were compared with the limits set for each cultivar. A cultivar was considered tolerant to expected climatic conditions when the indicator values resulted above critical values in at least 90% of realizations. While Riccardi et al. (2011) did not further specify the climate scenarios and realizations in terms of changing mean or climate variability, such analysis could be easily linked to the soil water availability indicators and the related limits for cultivars under climate change.

6.4 Conclusions

In this review, we have emphasized that changing climatic variability and the resulting extreme (climatic) conditions are highly relevant for different plant processes at different scales in comparison to changes in mean climate (although mean and variability may not be fully independent of each other). We have also shown how to quantify responses of plants to changing climate variability: While experiments seem to be well-suited to study the effects of changing climatic variability it is important to remember that they only control a limited number of factors. For modeling studies we stress that the model structure should allow integrating extreme events (e.g. by having the appropriate temporal resolution). These points highlight the importance of linking experiments, observations, and modeling studies as well as assessing study results in light of the background variability of the system and the temporal scale considered. We also identified several research gaps. While knowledge of plant responses to changing climatic variability for individual processes has to be consolidated, we still lack knowledge on how interactions of these processes and other environmental variables play out at different hierarchical levels and in combination with changing mean climatic conditions. Similarly, while there is room to improve individual methods to study changing climatic variability, there is a particular need to integrate observations, experiments and model results across scales.

Ultimately, the information on extremes and corresponding vulnerability of plants are crucial to identify which species and regions (and thus which ecosystem services and functions) are most at risk from climate change. Moreover, designing ecosystem-based adaptation strategies to climate change relies on understanding the interactions between species' natural adaptive capacity and climate change. Analyzing plant responses to climate variability is important to determine drivers of ecosystem dynamics over time (slow vs. fast

processes) and highlights the importance of extremes to assess the impacts of environmental change on social-ecological systems.

6.5 Acknowledgements

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7 Climate change adaptation and sustainable regional development: a case study for the Federal State of Brandenburg, Germany[6]

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Abstract

Located in a relatively dry region and characterized by mainly sandy soils, the German Federal State of Brandenburg (surrounding the capital city of Berlin) is especially vulnerable to climate change impacts (e.g. summer droughts) and cascading effects on ecological systems (e.g. decreasing ground water tables, water stress, fire risk, productivity losses) with socioeconomic implications. Furthermore, a complex interplay of unemployment, rural exodus, and an aging population challenges this structurally weak region. We discuss adaptation measures that are either implemented or planned, as well as research into adaptation strategies to climate change for the sectors forestry, agriculture, and water management as well as in nature conservation in light of socioeconomic and ecological challenges and benefits. In doing so, we adopt a systemic view of Brandenburg where the sectors discussed are seen as subsystems embedded in a larger regional system. This at least partially holarchical approach enables the identification of conflicts between adaptation measures, but also of synergies among the sectors that pertain to successful adaptation to climate change. The insights gained ultimately highlight the need for cross-sectoral, adaptive management practices that jointly target a sustainable regional development.

Keywords: Adaptation, Brandenburg, Climate change, social-ecological systems, sustainable regional development

7.1 Introduction

Past greenhouse gas emissions and the inertia of the climate system lead to a temporal mismatch between the effects of mitigation and already occurring impacts of climate change (Pielke et al. 2007). Additionally, current mitigation pledges would not limit warming to less than 3°C while the amount of funding made available for adaptation covers climate change impacts up to only 1.5°C of warming (Parry 2010). Although such a general number for global adaptation can only be a rough approximation and refers only to the financial dimension of adaption, it illustrates a large 'adaptation gap'. The currently observed and projected impacts of climate change (Füssel 2009; Smith et al. 2009), their combination, and their connection with other stressors of global change may exceed the current adaptive capacity of individual sectors (Adger & Barnett 2009). Furthermore, societies are increasingly vulnerable to climate change impacts for other reasons than climate change such as rapid coastal population growth (Pielke et al. 2007). Thus, adaptation to climate change is an urgent need and increasingly important in climate policy (Beck 2011).

In contrast to climate change mitigation which is intrinsically linked to the last 20 years' climate policy and which is a global process, adaptation to changing environmental conditions has always been part of human development and tailored to local or regional conditions depending of the scale of the impacts (Klein et al. 2005; Adger et al. 2007; Dovers 2009; Olmstead & Rhode 2010). Consequently, adaptation to extreme events (e.g. floods or droughts) has been considered more important than coping with long-term changes in average climatic conditions (Adger et al. 2007; Berrang-Ford et al. 2010). However, opinions on whether 'policy windows' induced by extreme events constrain or facilitate adaptation diverge (Adger et al. 2007).

Despite an increasing body of scientific literature on adaptation (Arnell 2010), documentations of explicit climate change adaptation actions in human systems are rare (Berrang-Ford et al. 2010). It is evident, however, that high adaptive capacity does not necessarily translate into action (Adger & Vincent 2005; Adger et al. 2007) and even forestry projects for climate change mitigation (i.e., planting trees to 'remove carbon from the atmosphere') seldom consider adaptation to climate change in their management plans (Reyer et al. 2009) despite their necessarily longer-term outlook. This lack of documentation is striking, particularly since many possible climate change adaptation actions can be justified for other reasons than climate change (Adger et al. 2007; Dovers 2009): Related to forest adaptation, this could be a diversification of forest species and structures to improve stability, biodiversity, and attractiveness for visitors (Knoke et al. 2008).

Each field is developing ways to adapt to global (climate) change (e.g. see Spittlehouse & Stewart (2003) or Seppälä (2009) for forestry or Hannah et al. (2002) or Lawler (2009) for nature conservation). Adaptive capacity is not equally distributed within societies (Adger et al. 2007), and stakeholders such as companies and corporations as well as public households which are potentially impacted by climate change need to develop appropriate adaptation measures. How adaptation strategies will be developed and implemented on regional and local levels is still being discussed controversially. The participation of stakeholders in the development of such strategies has been emphasized in many publications (e.g. Dessai & Hulme 2004; Füssel 2007). Methods for engaging various stakeholder groups in climate adaptation have been tested in dialogue exercises on sectoral adaptation (Hoffmann et al. 2011). Moreover, for adapting forests to climate change, for example, Bolte et al. (2009) suggested an integrative concept of adaptive forest management which addresses different scales: Species/provenance suitability assessments to be conducted at an *international scale* covering the distribution ranges of native and non-native species and their provenances. Priority mapping of adaptation strategies and respective decisions on where to intervene first on the *national or regional scale*. At the *local scale*, forest practitioners are finally responsible for the implementation of specific on-ground adaptation measures.

Moreover, adaptation measures in individual sectors may conflict with adaptations in other sectors and/or may entail direct or indirect social and environmental problems in other sectors or areas (Adger et al. 2007). Similarly to situations where current management practices exacerbate climate change impacts (Hulme 2005), Turner et al. (2010) point out that adaptation by humans may be a greater threat to natural systems than climate change itself. Theoretical approaches to adaptation thus call for concerted, cross-sectoral and multidisciplinary adaptation strategies that fit into a broader framework of sustainable development and regional values and that address the entire cascade of climate change impacts from the climate to social systems to avoid maladaptation (Burton et al. 2002; Adger & Barnett 2009; Barnett 2010).

We explore these considerations for the example of the Federal State of Brandenburg in Germany, which is suitable because it is situated in a vulnerable position close to an ecotone with projected climate shifts exacerbating current problems and it surrounds Germany's capital city of Berlin. Detailed regional studies show that climatic conditions that were exceptional in the past will become more common in the future (see section 7.4). Environmental problems, however, also have a socioeconomic dimension (e.g. the impact of demographic changes on land-use changes); climate change can be seen as a potential social

and political crisis (Leggewie & Welzer 2009). Our planet is seeing multiple major processes of change (Kunstler 2005). It is important to be aware of the complex synergies and non-linear changes both in environmental and in social systems (or social-ecological systems), and "multiple stresses in social systems can lead to runaway political chain-reactions" (Ibisch & Hobson 2010) if the changes are severe and transgress adaptive possibilities. Such considerations can be applied to larger political entities as well as to regions. The future of a region like Brandenburg is not only shaped by climatic changes but also by the developing social and economic changes at regional, national and global scales. For instance, Brandenburg's development perspectives also depend on the outcomes of the globally arising transformations in the energy and food production systems. Potentially rising prices as well as financial and economic crises caused in other sectors could cause decreasing availability of public funding and will potentially be ever more relevant drivers of regional policy.

The ultimate aim of adaptation research in Brandenburg is to answer the following question: What are the appropriate strategies for adapting Brandenburg to the various and partly uncertain impacts of complexly related global changes? The objective of this review is to discuss both implemented and planned adaptation measures as well as research into adaptation strategies to climate change in Brandenburg in light of the socioeconomic and ecological challenges and benefits associated with them.

Although adaptation pertains to many fields and parts of society (Klein et al. 2005), we focus on land and water resources and in particular the three sectors forestry, agriculture, and water management as well as on nature conservation, which takes place in all the aforementioned sectors. We do not explicitly consider adaptation of infrastructure, the transport, energy or health and security sector. We follow the adaptation framework developed by Burton et al. (2002) insofar as we account for past and future trends in both climatic and socioeconomic development.

After briefly defining the main terms and introducing a simple conceptual model, we introduce the Brandenburg region especially in light of demographic and climatic changes. We then line up the challenges, existing as well as planned and currently discussed approaches to adaptation, and recommendations and options for action in forestry, agriculture, water management and nature conservation. We then highlight conflicts and synergies between them and integrate these in the 'Brandenburg system'. Finally, we derive implications for sustainable development of the region as well as general conclusions.

7.2 Definitions

To apply these considerations, we rely on the following definitions which follow those of the IPCC (IPCC 2007b) if not indicated otherwise. *Adaptation* is "the adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities" (IPCC 2007b). Systemically, adaptation means small-scale shifts that result in the emergence of meta-states that are new operating points; under extreme conditions, this shift can induce dramatic changes to systems' complexity, functions and characteristics (Hobson & Ibisch 2010). From this perspective, there can be even an adaptive simplification and degradation of systems. However, sustainable development in a changing environment implies that ecological and (dependent) social systems shift to new operating points without dramatically and abruptly changing functionality and characteristics (Ibisch 2010; Hobson & Ibisch 2010). Adaptation can be proactive (i.e., anticipatory) in character, autonomous (i.e., spontaneous without "conscious response to climatic stimuli but triggered by ecological changes in natural systems and by market or welfare changes in human systems"), or planned through "deliberate policy decision" (IPCC 2007b). We do not limit our analysis to specific classes (autonomous, planned reactive…) or categories of adaptation measures (such as technological, economic, etc., see Adger et al. 2009) but to those which are relevant in Brandenburg across these classes and categories. Furthermore, *sensitivity* describes "the degree to which a system is affected, either adversely or beneficially by climate variability or change," whereas *adaptive capacity* is the "ability of a system to adjust to climate change (including climate variability and extremes) to moderate potential damages, to take advantage of opportunities or to cope with the consequences" (IPCC 2007b). Adaptive capacity is a function of financial means, education, infrastructure, social capital, etc. Having adaptive capacity does not necessarily mean that this capacity is used. *Vulnerability*, however, is "the degree to which the system is susceptible to, and unable to cope with, adverse effects of climate change" (IPCC 2007b). *Resilience* describes the "ability of a social or ecological system to absorb disturbances while retaining the same basic structure and ways of functioning, the capacity for self-organization, and the capacity to adapt to stress and change" (IPCC 2007b). Despite these clear definitions, these concepts are in reality interrelated, context-specific and differ in time and space, as well as between social groups (Smit & Wandel 2006). Finally, *adaptive management* aims at preserving and developing the functionality of a system while continually monitoring and evaluating the success of management measures (Gunderson & Holling 2002).

7.3 Conceptual model for analyzing adaptation measures

While there have been many efforts to classify adaptation measures (e.g. Smithers & Smit 1997; Smit et al. 1999; see discussion by Eastaugh et al. 2009), theoretical frameworks to study synergizing and conflicting effects of adaptation measures in between sectors as well as interactions between adaptation measures have only been tackled marginally (e.g. in Füssel 2007; Moser & Ekstrom 2010). To organize our examples of adaptation measures as well as their effects and linkages and to foster therewith the transfer and generalization of our outcomes, we constructed a simple conceptual model (Fig. 7-1). Fig. 7-1 now shows all possible interactions: (1) A positive influence, that is, the adaptation measure enhances the ecological, economic, or social conditions of a sector. (2) A negative side-effect, that is, the adaptation measure deteriorates the ecological, economic, or social conditions of a sector. (3) A positive side-effect, that is, the adaptation measure enhances the ecological, economic, or social conditions of a sector. While (1) is usually the 'wanted' effect of an adaptation measure, the interaction of (1) and (2) and (1) and (3) results in a conflict or a synergy, respectively. These can either be inter-sectoral if different sectors are affected but also intra-sectoral if for example the adaptation measure enhances the economic but deteriorates (or enhances in case of a synergy) the ecological conditions within one sector. It is important to note that the weight of the positive and negative effects may not be equal. Thus, conflicts may cover a broad range of interactions from 'low-regret' (Wilby & Dessai 2010) to severe conflicts, where the negative side-effect may be much stronger than the expected positive effect. Similarly, the strength of a synergy varies. Finally, Fig. 7-1 also shows that there may be positive or negative interactions between two distinct adaptation measures. Throughout this document, we refer (explicitly or implicitly) to this conceptual framework to structure the examples of conflicts and synergies of adaptation measures.

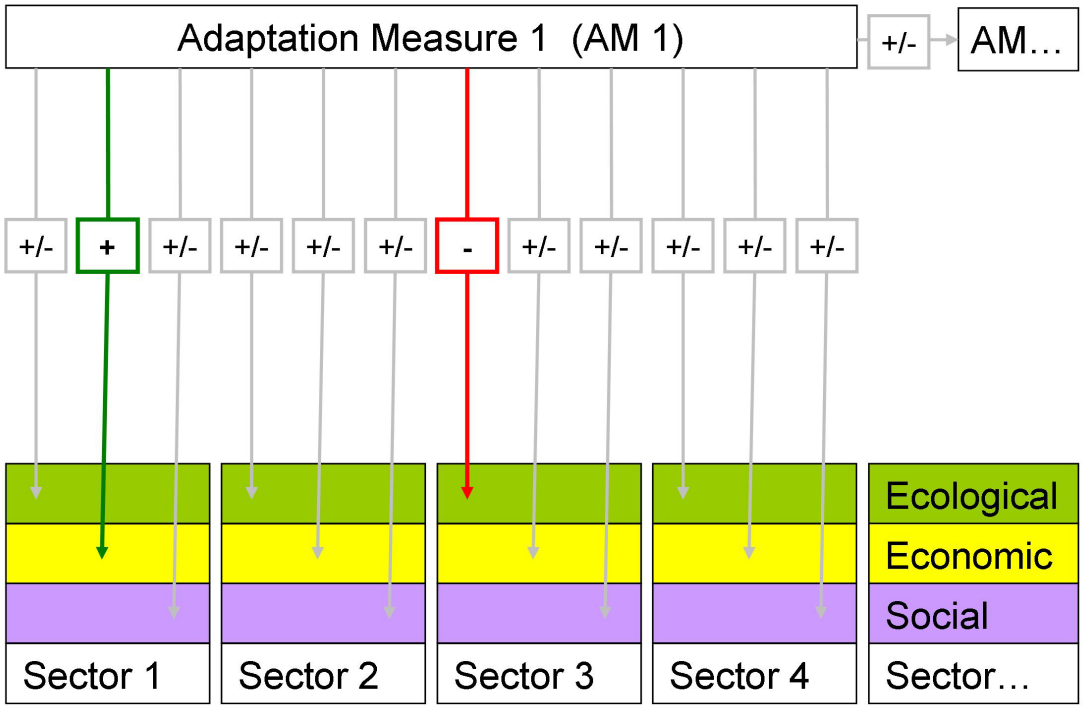

Fig. 7-1 Conceptual model of conflicts and synergies of adaptation measures. The arrows depict possible positive or negative effects an adaptation measure may have on ecological, economic or social aspects of a sector. In the figure, the particular example of adaptation measure 1 having a positive effect on economic aspects of sector 1 (i.e., the 'wanted effect') while having a negative effect on ecological aspects of sector 3 highlights a conflict. For a description of other possible interactions, see the text.

7.4 Brandenburg's past and possible future socioeconomic and climatic development

Brandenburg is the fourth largest German federal state (29 481km^2), located in the geographic region 'Northeastern German Lowlands', and encircling Berlin (ASBBB 2009). Its landscape and soil formation result from several glaciations during past ice-ages and are characterized by sandy and poor soils (Büchner & Franzke 2009). Half of the total area is nowadays agricultural land (Fig. 7-2e) with 10% of it being used for organic farming, Brandenburg, in comparison with the other Federal States, maintains the highest share of this land-use type in Germany (ASBBB 2009; Statistisches Bundesamt 2010). The forest area of Brandenburg (including Berlin) is 35.3%, which is more than the German average of 31% (BMELV 2006) and consists mostly of stands dominated by coniferous trees (Fig. 7-2e). Whereas biomass for bioenergy generation from forests does not constitute an important part of forest production and is likely to decline in the future, bioenergy generation with biomass from short rotation coppice and agriculture is likely to increase (MUGV 2010). More than 40% of the total area is under a varying degree of nature protection (ASBBB 2009; Fig. 7-2d). The population density reflects the rural character of Brandenburg: With a population

density of 86 inhabitants/km^2 it is the second-last populated federal state (cf. German average 230 inhabitants/km^2) and in the last years, a rural exodus of young people and declining birth rates combined with increasing life expectancy led to a decreasing and rapidly aging population (ASBBB 2009; Fig. 7-2f). The worsening economic situation in the late 90s after a brief post-reunification increase in salaries and GDP (Büchner & Franzke 2009; Baten & Böhm 2010) and the about 63% higher unemployment rate than the German average rates for the period 1994-2009 (Bundesagentur für Arbeit 2009) explain these demographic trends to a large extent (Büchner & Franzke 2009). The demographic development will strongly influence the future of Brandenburg (Büchner & Franzke 2009). Although the number of employees in the primary sector (forestry, agriculture, and fisheries) has strongly decreased in the last 20 years, this sector is still a quite important employer in Brandenburg in comparison with the German average (4% in BB versus 2% in Germany; ASBBB 2009). A special feature is the location of the German capital Berlin with 3.5 million inhabitants in the center of the federal state. Brandenburg provides a surrounding landscape for Berlin for recreation, ecosystem services, and transport.

On top of the described changes and their repercussions, the following climatic changes have been observed and projected in this already warm and dry state (Fig. 7-2a, b). Wechsung et al. (2008) analyzed climate change in Brandenburg. The analysis of the observed climate from 1951 till 2003 in Brandenburg states an increase of the annual mean temperature varying between 0.6 and 1.4K, with annual averages for this period varying from 7.8 to 9.5°C. This trend of temperature increase is noticeably higher than the global mean temperature trend. Furthermore, Brandenburg is characterized by low annual precipitation sums compared with other German regions, on average clearly below 600mm during the last 50 years. The trend for the period 1951-2003 is statistically not significant; there are regions in Brandenburg with decreasing annual precipitation sum and others with increasing precipitation sum. However, the seasonality of precipitation is changing toward decreasing precipitation sums during summer and increasing precipitation sums during winter. Furthermore, annual soil water shows a decreasing trend for the period 1955-2003 (Holsten et al. 2009; Fig. 7-2c).

Various studies analyzed regional impacts of projected global climate change in the twenty-first century in Brandenburg (Gerstengarbe et al. 2003; Wechsung et al. 2008; Linke et al. 2010; Linke & Stanislawsky 2010). These studies used climate change projections from Global Circulation Models (GCM) driven with scenarios published by the IPCC (2001), especially the A1B CO_2 emission scenario. Global climate change scenarios were regionalized

using statistical regional climate models (STAR (Orlowsky et al. 2008) and WettReg) or dynamic regional circulation models (CCLM, REMO) (Linke et al. 2010). It is important to note that each of these models has their own limitations which are relevant for impact studies and consequently also for adaptation planning (see review by Fowler et al. 2007). Applying the A1B scenario, simulated with the GCM ECHAM4 or ECHAM5, these studies project a temperature increase of 1-2K in Brandenburg until 2050-2060. The regional model projections indicate a continuing decrease in precipitation sum during summer and an increase during winter. A decline of the climatic water balance could be the consequence of the temperature and the precipitation trends yielding negative values during the vegetation period.

7.5 Approaches and strategies to climate change adaptation

The federal state government of Brandenburg, advised by its 'Council on Sustainable Development and Resource Protection', has developed a position paper for a sustainable development strategy (MUGV 2011) and a catalogue of possible adaptation measures (MLUV 2008). The former highlights the need for adaptation in all sectors and refers to the latter, which is, however, neither prescriptive, nor bound to specific temporal or spatial scales. In the following, we present existing and presently discussed sectoral approaches from scientific articles, reports, publicly available agency documents and other sources.

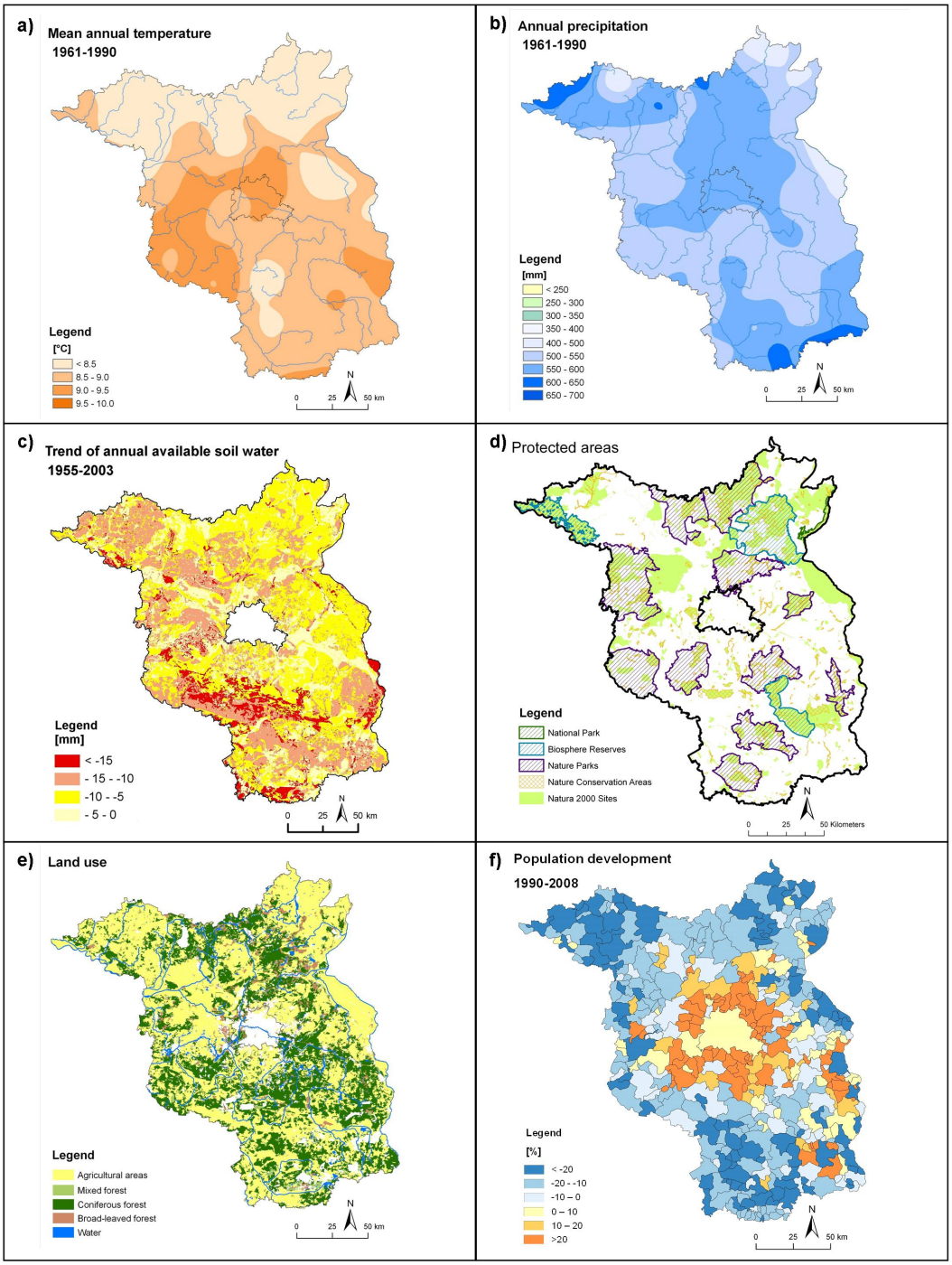

Fig. 7-2 Current climate, hydrological, and demographic situation and land use in Brandenburg: a) mean annual temperature (1961-1990), b) annual precipitation (1961-1990) (temperature and precipitation data of the German Weather Council processed at PIK in 2010), c) simulated trend of annual available soil water from 1955 to 2003 (modified from Holsten et al. 2009, d) protected areas (data from the Federal Agency for Nature Conservation), e) land use (data from the CORINE Land Cover 2000 data set of the Federal Environment Agency) and f) demographic trends (modified from the cartographical service 'Strukturatlas Brandenburg' of the State Office for Building and Transport).

7.5.1 Forestry

Forest ecosystems in central Europe face considerable impacts of climate change (Lindner et al. 2010) and forest management has to find ways to adapt without the spatial and temporal extent of these impacts as well as their interactions being fully understood. While regional climate change may induce an increase in forest growth (Lasch et al. 2002) which is a potential advantage of global change, it remains unclear under which conditions productivity increases will occur, which species will benefit the most, how long the productivity increase will last and what the interactions with disturbances are. Since forests and forestry are an important part of Brandenburg's landscape and rural economy (see section 7.4) the adaptation of forests and forest management is of high concern to regional decision makers and stakeholders. The 'Eberswalde Declaration', the result of a conference bringing together actors from more than 70 different institutions, administrative bodies, and associations in 2008, highlighted 11 statements that stress the importance of active adaptation (Spathelf et al. 2008). Generally, forest management practices are already available that enhance the adaptive capacity of forests (see also Table 7-1; Spittlehouse and Stewart (2003); Seppälä (2009)). Site-specific tree species selection has been a fundamental principle of forest management in Germany for decades. Additionally, in the last 20 years, close-to-nature silviculture has become the dominating approach for shaping the forests toward a better presence of a region's natural species, more natural regeneration as well as stable and diverse mixed stands (von Lüpke 2004; Röhrig et al. 2006). Thus, the large-scale, monospecific, and mostly coniferous forests in Germany were and shall be gradually converted into mixed broadleaved/coniferous stands. The greater resilience and stability of site-adapted, species-rich and structured forests has been proven several times (see the review by Knoke et al. 2008). Furthermore, inter-specific competition in mixed forests may to a certain degree shelter some species (e.g. European beech (*Fagus sylvatica*)) from the effects of drier and warmer conditions of a changing climate (Reyer et al. 2010).

Whereas globally, forest agencies seem to be in an early stage of adapting forest management to climate change (Eastaugh et al. 2009), Brandenburg's forest administration already pursues programs with important adaptation aspects. Since the 1990s, the forest administration of the Brandenburg region is promoting the conversion of the still dominating pure Scots pine (*Pinus sylvestris*; 73% of forest area) forests for ecological reasons such as lower susceptibility to storm, fire, and insect damage (MLUV 2007). The forestry section of the 'Catalogue of countermeasures for climate change mitigation and adaptation of the federal state government' (MLUV 2008) focuses on forest conversion toward diverse forests,

with small-scale species mixes adapted to micro-site conditions and greater importance given to secondary species. In practice, this leads to an insertion of broadleaved trees (primarily oaks (*Quercus robur*, *Quercus petraea*) and European beech) into the mono-specific pine plantations, mostly by underplanting in groups. The current area of convertible pure pine stands in Brandenburg amounts to 150 000ha (roughly 15% of the forest area). Various research projects such as 'Oakchain' (Elmer et al. 2009) or 'Zukunftsorientierte Waldwirtschaft' (MLUV 2005) have not only addressed the ecological benefits of forest conversion but also its effects on the entire wood production chain of custody and even explored alternative possibilities of wood utilization such as 'thermowood', that is, thermally treated wood to substitute tropical timber.

Besides converting mono-specific coniferous plantations into mixed broad-leaved forests, there is a portfolio of potential measures for adapting silviculture and forest management to global change at the stand level, such as adjusting rotation length, species and provenance choice, thinning strategy and type of regeneration (Bolte et al. 2010). These measures are often discussed in light of their economic, social and ecological impacts. Among practitioners and especially private forest owners, there is substantial debate on the future role of non-native species, such as Douglas-fir (*Pseudotsuga menziesii*). In general, several exotic tree species (besides Douglas fir e.g. red oak (*Quercus rubra*), black locust (*Robinia pseudoacacia*), grand fir (*Abies grandis*)) performed well in terms of growth in Brandenburg in the last decades (Bolte et al. 2010) and are from an economic point of view interesting alternatives to current species. The opinions on Douglas-fir among forest stakeholders range from euphoric support of timber producers to requests from forest conservationists to ban and completely eradicate this non-native species. Emotional and ideological arguments dominate this debate, and alternative approaches such as a careful replacement of the 'non-native' versus 'native' species concept by a 'damage criterion' approach as presented by Warren (2007) are not pursued. Douglas-fir outcompetes native species in terms of growth and its climatic amplitude, especially its lower susceptibility against summer drought, means that it is likely able to cope with a certain degree of climate change (MIL 2009). However, considerable uncertainties regarding its water requirements and natural enemies remain. Especially the main insects damaging Douglas-fir do not occur in Europe yet but are likely to prosper under future climates (Verkaik et al. 2009). In Brandenburg, currently about 1% of the forest area is covered with Douglas-fir-mixed forests or mono-specific stands of a mean size of 1ha, but the perspective of the state forest administration is to increase this proportion to 5% (MIL 2009). In the case of Douglas-fir, organized and structured

communication and participation based on a sound theoretical framework of stakeholder involvement would support judging this adaptation measure.

In general, a forest which offers a variety of different management options for the future in terms of tree species, structure, intervention measures and which is integrated in a landscape management framework will more likely be a resilient/stable and less vulnerable forest (Bodin & Wiman 2007; Millar et al. 2007). Furthermore, such forests provide multiple goods and services as increasingly valued by society (Bengston 1994).

7.5.2 Agriculture

Agriculture plays a pivotal role in human societies since it provides food and livelihoods. Therefore, its adaptation to climate change is crucial. Many adaptation measures apply to all forms of agriculture since the basic underlying problems are similar and generic to land as a production system. However, since the process of adaptation in organic agriculture tends to be much more complex and difficult than in conventional agriculture (Rahmann 2008) and since Brandenburg shows the highest proportion of organic farming in Germany (10%), we focus our analysis on this category (if not indicated otherwise) to gain insight into the full scope of adaptation challenges and opportunities. Nonetheless, the main findings outlined below (reduced tillage) pertain also to conventional agriculture in slightly modified form.

As shown in section 7.4, farmers in Brandenburg cultivate fields that primarily tend to be characterized by sandy soils with low available water capacity and severe sub-soil compaction. This highlights the strong sensitivity of organic as well as more traditional farming particularly to the projected climate change impacts in Brandenburg, warming and decreasing summer precipitation (see section 7.4). One of the main reasons for the vulnerability of organic farming systems besides reduced water availability during summer droughts is the nitrogen limitation of these systems. Nitrogen supply of organic farming systems is particularly susceptible under expected climatic changes: On the one hand, dry early-summer periods reduce the nitrogen mineralization (Stanford & Epstein 1974; Leiros et al. 1997), which may result in significant nitrogen deficiencies and yield losses especially in winter wheat. On the other hand, increasingly mild and humid winters increase the risk of nitrate losses through enhanced mineralization and leaching (Fig. 7-3; Stanford & Epstein 1974; Lükewille & Wright 1997; Rustad et al. 2001; Thomsen et al. 2010). The limitation of the nitrogen supply is further aggravated as the forage supply is extensively based on in-farm forage production with legume-grass swards according to the organic farming guidelines (EC 2007a). Thus, forage losses caused by drought periods or intense rain events

can only be compensated by expensive bought-in forage. Moreover, forage deficiencies imply a significant reduction of nitrogen input. Short-term reactive adaptation measures for the optimization of the water and nitrogen supply such as the application date and amount of mineral nitrogen fertilizer or feed purchase are strongly restricted in organic farming. Above all, the use of evaporation-reducing mulch systems is largely excluded due to the prohibition of total herbicides. Therefore, the challenging task is to improve the water and nitrogen supply for Brandenburg's organic farms to minimize climate change-related risks and impacts.

Generally (and not only restricted to organic farming), existing farming system types differ significantly in scale, intensity, and efficiency, therefore requiring a broad portfolio of adaptation measures (see also Table 7-1). Besides (1) the selection of cultivars tolerant of water stress, (2) adapted pasture management of hydromorphic grasslands and (3) agroforestry systems (for more adaptation options see Bindi & Olesen 2011), the regionally most important and promising adaptation strategies of agricultural management aim at reducing tillage to reduce soil erosion, improving water infiltration, reducing evaporation and improving soil structure. Semi-quantitative approaches to assess climate impacts and support strategic decisions are also important adaptation measures (e.g. Schaap et al. 2011).

Due to the restrictions in organic farming systems mentioned, adaptation measures for organic cropping systems must primarily rely on strategic long-term planning. Therefore, reduced soil tillage combined with modified tillage and sowing dates and catch crop use are being developed and tested as adaptation measures. An altered tillage device (e.g. a ring cutter) aims at preserving the soil structure, allows a shallow overall root-cutting thus enhancing infiltration, increasing soil water availability, and reducing soil erosion through surface run-off. Simultaneously, shallowly incorporated crop residues reduce evaporation and increase earthworm activity. In comparison, conventional plow tillage increases the soil's susceptibility to erosion, compaction, and water losses (Eitzinger et al. 2009). Despite these inconveniences, organic farmers use plowing as a standard measure for controlling perennial weeds and to kill legume-grass swards effectively. Above that, the intensive loosening of the top soil increases the microbial nitrogen mineralization within the main growing period, resulting in higher yields (Kahnt 2008). Summer crops can be well established in time also under wet soil conditions, where plowing would probably cause further soil damage. Furthermore, the establishment of legume grass and cover crops on dry soils in summer could be improved by minimizing evapotranspirational water losses. These

advantages of a new device such as a ring cutter exemplify that there are new management options for climate-adapted crop production.

These climate-adapted production activities can be integrated into PC-based cropping system planner (e.g. ROTOR of Bachinger & Zander 2007) and can, in combination with site-specific risk assessment for forage and nitrogen supply, support cropping planning decisions. To introduce new devices such as a ring cutter, communicating their advantages and discussing their application with stakeholders are crucial. This will increase the adaptive capacity of Brandenburg's organic farming sector.

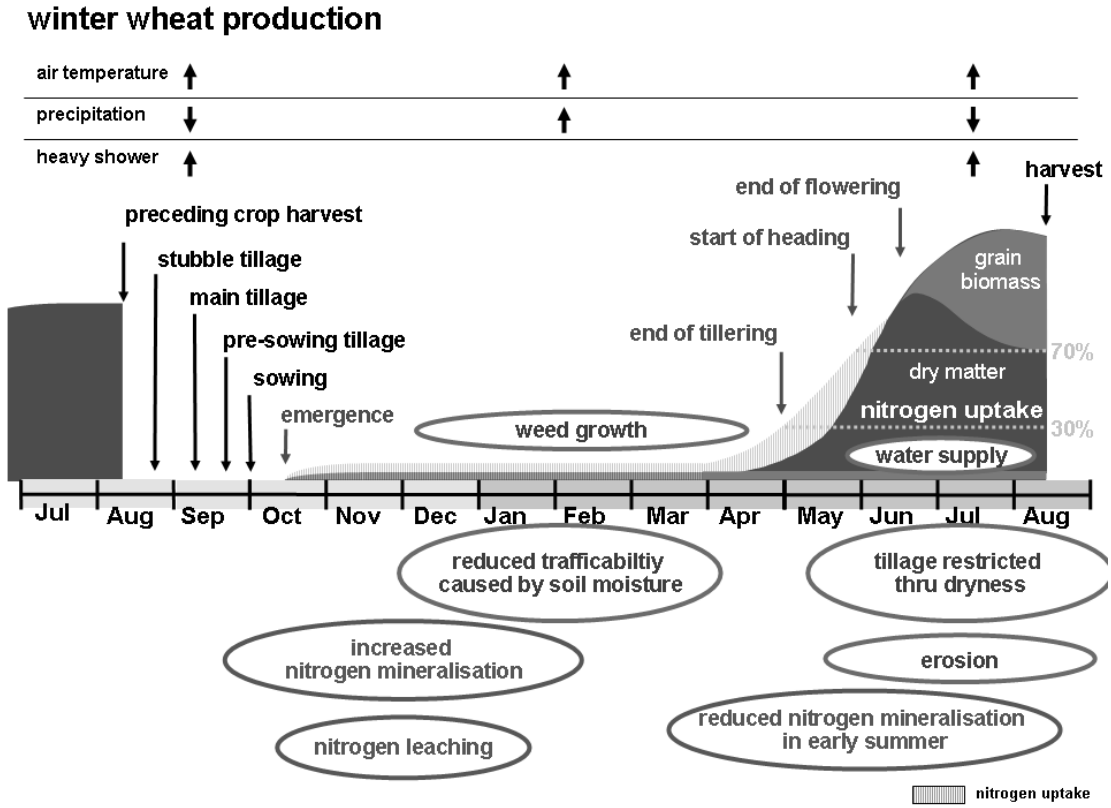

Fig. 7-3 Climate change impacts on cropping planning of winter wheat production. The bold arrows at the top of the figure indicate seasonal climate changes, whereas regular arrows in black indicate management interventions and regular arrows in grey indicate phenological events.

7.5.3 Water management

In an already dry region such as Brandenburg, which faces even drier future summers, managing water is crucial. In Brandenburg, climate change impacts on water resources and the future development for hydrological extremes (floods and droughts) are among the main concerns. Many recent investigations (e.g. Huang et al. 2010) highlighted the challenges that result from shifts in precipitation patterns and snow regime, changes in seasonal water availability and water quality, rise of sea level, and increase in the frequency and/or intensity of river floods and droughts, all coupled with the rise in mean surface temperature. The

State of Brandenburg has been struck by several severe river floods in the last 15 years, and the scenario projections show that the intensity of floods will most likely increase under climate change (Hattermann et al. 2011). Furthermore, as discussed in the previous sections, the water sector strongly interacts with forestry and agriculture, and water management is therefore a cross-sectoral issue.

Similarly to the other sectors, general adaptation measures are available. Table 7-1 lists possible technical and management strategies to adapt to regional climate change in the water sector (for a larger set of possible measures cf. Kabat et al. 2002). Most of the measures proposed also help to adapt to the already observed climate variability such as an already carried out or planned raising and relocation of dikes and can thus be classified as 'no (or low)-regret measures'. Another measure discussed in the framework of climate change adaptation, especially to counteract droughts and desiccation of the upper areas of the catchment, is water retention in the landscape to minimize run-off to the sea and to counter decreasing ground water tables. Therefore, water retention and rewetting measures such as those carried out primarily for nature conservation (e.g. in the nature reserve Naturpark Uckermärkische Seen, (Mauersberger 2010)) may entail important cobenefits for adaptation and also mitigation (e.g. by fostering peat formation). The appropriateness of these selected measures and the feasibility of their implementation taking the local characteristics of the natural and social environment in Brandenburg into account have to be discussed in a regional context.

Combinations of technical and management measures represent an appropriate strategy to adapt to climate change because they can be implemented within a single sector and at the local or regional scale. Although they are often meant to decrease the vulnerability to climate change of a single sector or region, they most often affect also the vulnerability of other sectors or regions in a positive or negative way. This can lead to conflicts among different users (cf. section 7.6.1). Therefore, an integrated approach to water resources management (IWRM), especially if it involves relevant stakeholders in the decision-making process, is very important to provide a sustainable and widely accepted management solution (but see also Huntjens et al. (2010) for limitations). Such IWRM at the catchment scale involving the relevant upstream and downstream stakeholders and experts is the backbone of both the EU Water Framework Directive (EC 2000) and the EU Flood Directive (EC 2007b). It is therefore very advisable to link the process of designing management strategies to adapt to climate change with the implementation of these directives (Hattermann et al. 2008).

7.5.4 Nature conservation

Due to its natural setting, political circumstances and economically unfavorable conditions throughout centuries, Brandenburg, in western Central European terms, has enjoyed a relatively low level of anthropogenic pressure (e.g. population density, land take rate, pesticide use, etc.) on its biodiversity (BfN 2008). Ecosystems in Brandenburg are thus in a better conservation state (e.g. river water quality; LAWA 2000) than the German average. Nevertheless, Brandenburg's biodiversity is facing substantial pressures from various stressors such as habitat degradation, fragmentation, and loss. Climate change is emerging as an additional anthropogenic threat and as it is expected to gain velocity, it is prudent to assume that it will interact with the 'conventional' stressors mentioned. The only imprecisely predictable pathway of climate change as well as of societal reactions to it, such as the potential spread of bioenergy crops, and other aspects of global change will together increase planning uncertainty.

Society in Brandenburg through its governments has chosen to address these pressures through the creation of a protected area system of exceptional coverage (e.g. 26.5% of the territory under more or less strict protection as Natura 2000 sites, the top score of all German states; BfN 2008). The general nature conservation approach is widely static (attempting to preserve remnants of historical cultural landscapes) and segregative, rendering the matrix exposed to increasingly unsustainable use and development. Nature parks and biosphere reserves actually are designed to integrate land use and conservation. However, this approach has lately been weakened by segregatively prioritizing Natura 2000 sites enclosed in them (Ibisch & Kreft 2010a). Management of Natura 2000 sites in Brandenburg is complicated by attribution of all those sites enclosed in larger protected areas to the Environmental Agency and those sites outside other protected areas to the Nature Conservation Fund. The landscape framework plans ('Landschaftsrahmenpläne') of the municipalities represent another scale and approach to (potential) conservation management.

The landscape planning for the whole landscape was thought to represent a strong instrument of integrative conservation even outside protected areas, but in practice commonly fails to guide socio-economic development driven by productive needs and investment opportunities.

Currently, conservation management planning in Brandenburg generally revolves around very detailed prescriptions for treatments (mowing, grazing, logging, etc.) of often small to

very small areas that represent narrowly circumscribed remnants of the historical landscape. The elaboration of management plans by contracted specialized consultants is laborious and takes some 1-3 years, depending on the complexity of the site. Once it is completed, a management plan is meant to serve between 6 and 10 years (varying between protected area categories).

Adaptation to climate change (see also Table 7-1; Hannah et al. (2002); Lawler (2009)) has not yet found its way into conservation management planning in Brandenburg. At the present, however, conservation managers might be in the process of intuitively becoming more sensible toward accelerating environmental changes – the existent long planning cycles, which do not allow for intermittent adaptations of management, are increasingly criticized as too inert and thus impractical (H. Mauersberger, M. Petschick, L. Thielemann, pers. comm.).

Increased planning uncertainty calls for a proactive-adaptive approach to nature conservation that ultimately serves to enhance the resilience of biodiversity and to reduce its vulnerability (Ibisch & Kreft 2009; Ibisch et al. 2010). Bringing together the 'dispersed' conservation planning and management regimes under one roof would obviously facilitate a spatially as well as institutionally more coherent management strategy. Fundamental contributions to adequately addressing this challenge lie in providing staff and funding that enable conservation administrations to adequately address complex protected area management issues, including climate change, and in properly designing management plans based on the identification of key vulnerabilities of a specific conservation site. Once the vulnerabilities are assessed, it will be possible to deduce adaptation measurements that allow for a proactive conservation management.

A key challenge to the success of protected areas is to reduce the vulnerability of the management. To this end, assessments should be directed to its relevant dimensions: the specific parts of biodiversity defined as conservation targets and associated conservation goals, the spatial conservation design as well as institutional infrastructures (Fig. 7-4; Ibisch & Kreft 2009, 2010b). Management options may then build upon the aspects identified as vulnerable in all these dimensions and aim at reducing their vulnerability.

Such vulnerability assessments should form part of systematic, adaptive management planning. The 'Open Standards for the Practice of Conservation' (CMP 2010) are built around an explicitly adaptive management cycle. Management designed under the 'Open Standards' is much leaner than the traditional multi-volume plans and thus both easier and more

transparent in its design and implementation. The tool is also inherently participatory, as they require the formation of a project team that comprises all stakeholders relevant for accomplishing of the goals set for the protected areas. As many threats to biodiversity often do not arise locally, but are of regional or even global character, and as the scope of solutions should be guided by natural boundaries (Fee et al. 2009), it appears prudent to invite stakeholders 'systemically', that is, to include representatives of the forces that influence energy and material flows within the natural boundaries the protected area is situated in.

Looking beyond these practical considerations, modern conservation approaches such as the ecosystem theory (Jørgensen 2006) do not consider nature conservation as 'land use' that occurs in a distinct, segregated sector. In this sense, conservation does not compete with other sectors, but it is rather a higher order interest in protecting biodiversity across scales and maintaining ecosystem functions and services. Hence, suggestions such as the (radical) 'Ecosystem Approach' (CBD 2010; Ibisch et al. 2010) are inherently integrative and offer an important framework for adaptation although they are thus far still in an early stage of implementation in Brandenburg (Fee et al. 2009). Current 'mainstream' lines of thought of adaptation of nature conservation to climate change which focus on ecological networks that allow the movement of animals and plants and thus range shifts of population and species can be easily embedded in such an adaptation strategy.

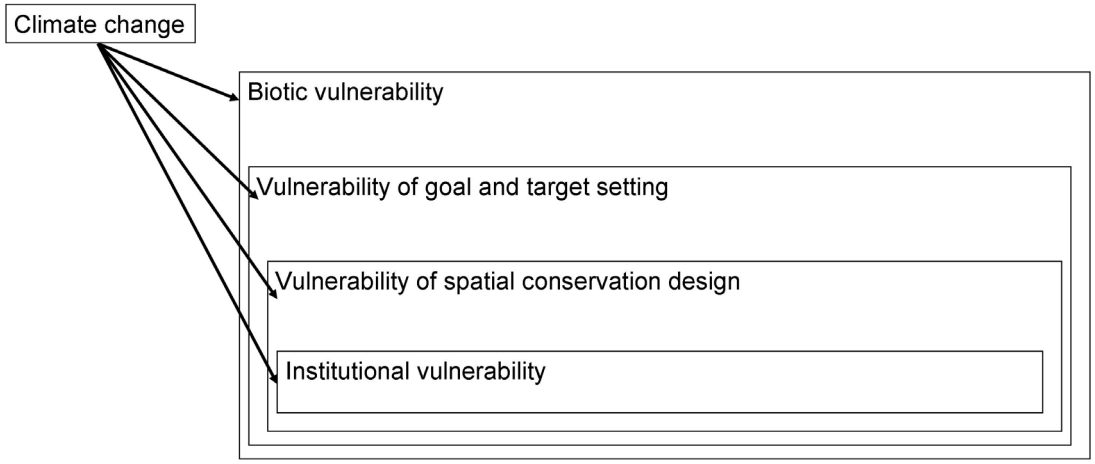

Fig. 7-4 The four dimensions of vulnerability of protected areas and other 'conservation systems' as affected by climate change (adapted from Ibisch & Kreft 2009).

Table 7-1 Potential adaptation measures and strategies in Brandenburg resulting from the references cited in the sections 7.5.1 to 7.5.4 and from the authors' personal experience.

Forestry

- silvicultural management:

-conversion of conifer plantations in close-to-nature forests
-species and provenance selection
-provenance trials
-management of stand densities and regeneration

- hydrological management (e.g. reduction of drainage)
- development and marketing of alternative wood products (e.g. 'Thermowood')

Agriculture/organic farming

- reduced tillage (e.g. ring cutter)
- strategic long-term planning (e.g. ROTOR)
- modified sowing dates
- catch crops

Water

- flood protection:

-improvement of technical flood protection (e.g. dikes, reservoirs, drainage systems)
-restoration of natural retention areas and increase of infiltration capacity
-restriction of settlement/building development in risk areas
-adjusting standards for building development (e.g. permeable surfaces, greening roofs)

- drought/low flow protection:

-improvement of technical measures to increase water availability
-increasing of water retention
-increasing efficiency of water use (e.g. leakage reduction, use of grey water)
-economic incentives (e.g. water pricing)
-restriction of water uses in times of shortage
-landscape planning measures to improve water balance (e.g. change of land use, forest conversion)

Nature conservation

- adoption and implementation of principles of CBD's Ecosystem Approach:

-adaptive management
-management in adequate dimensions of space and time
-acceptance of change (dynamic instead of static goal-setting)

- identification of and management for functional conservation targets and goals (e.g. water-retention, re-wetting)
- coherence/ better coordination and cooperation of protection initiatives
- reduction of institutional fragmentation
- enhancement of ecosystem connectivity

General adaptation measures

- awareness raising, information campaigns
- forming of financial resources
- improving risk assessments and general information flow
- improving insurance schemes against climate change damage

7.6 Systemic perspective on conflicts and synergies between adaptation measures and common practices or regulations

The adaptation measures mentioned above (see also Table 7-1) are all measures that are actually carried out, planned or under research to become operational. While this does not necessarily mean that they will be adopted, but they are all supported by some decision makers or stakeholder groups. At the level of Brandenburg (and sometimes even beyond), they may however conflict or offer synergies either with current practices or regulations or with other adaptation measures.

7.6.1 Conflicts

Since strong concerns over the future water availability are common not only in the water sector but also in forestry and agriculture, water management bears a strong conflict potential. Retaining water in the landscape (e.g. in wetlands or bogs for nature conservation) leads to an increase in evapotranspiration, as plants can satisfy their water demand from groundwater in periods with low water availability, especially in late summer. This substantially influences the discharge of rivers with implications for the transport (shipping) and other sectors (e.g. the energy sector) operating downstream. Thus, in reference to the conceptual model in Fig. 7-1, rewetting measures have positive effects on the ecological aspects of nature conservation but may negatively affect economic aspects of other sectors. Moreover, building reservoirs for drought and flood mitigation as well as rising and relocating dikes can have severe impacts on river ecology. Hence, inducing positive effects on social and economic aspects of the water sector threatens ecological aspects of the water sector and nature conservation. Furthermore, intensifying wood production (e.g. by inserting Douglas-fir in forests) under climate change may counter water-retention measures for an improvement of the regional water balance. Additionally, the use of non-native species such as Douglas-fir strongly conflicts with current concepts of nature conservation. Moreover, current, static nature conservation concepts and corresponding management planning generally collide with dynamic, proactive, and adaptive concepts (cf. section 7.5.4). Due to its overarching character, nature conservation is not only affected by climate change impacts on protected areas and individual species (see e.g. Loarie et al. 2009) but has to cope with natural resource use systems (such as forestry, agriculture…). Fields and forests connect protected areas but by reacting to climate change their managers raise directly or indirectly new threats to nature conservation goals (e.g. insertion of non-native, climate-

resilient species or increased biomass extraction on agricultural and forest land). Moreover, current practices and regulations and conflicting interests and values restrict several adaptation options much more than technological or ecological constraints: The certification rules in organic farming restrict short-term reactive measures such as buying extra forage and using mineral fertilizer or forest conversion threatens the steady supply of pine wood to the forest industry. This highlights the importance of 'social limits' to adaptation (Adger et al. 2009). Other conflicts are listed in Table 7-2.

7.6.2 Synergies

Similarly to the situation for conflicts, the most obvious synergies also relate to water management. Besides the positive effects of a rewetting of wetlands and bogs for nature conservation (e.g. restoration of habitats), these measures improve the regional water balance and help to buffer heavy rain events and floods (i.e., positive side-effects for water management, although rewetting is not primarily an adaptation measure). When floods occur, they ease the pressure on dikes. Furthermore, the building of reservoirs and improved reservoir management influences the hydrograph of the entire river and can improve drought mitigation (water release to augment low flows, water storage for irrigation) and also flood retention. These measures in the water sector also protect infrastructure and people.

An important economic cobenefit of forest conversion is that diverse forests provide a broader range of forest products and services. Most importantly, however, the adaptation measures of the individual sectors as well as the new view of nature conservation presented here all refer to an 'integrated management' and strategic long-term planning which includes communication with other sectors and stakeholder participation as an important adaptation measure. The climate change impacts combined with the socioeconomic challenges pose common threats to the individual sectors. This creates a truly cross-sectoral problem that establishes a common ground for discussion and action: Actors which are usually more or less opposed have now a common problem at the regional level which may constitute an important window of opportunity to improve communication and dialogues. Other possible synergies are listed in Table 7-3.

Table 7-2 Possible conflicts of adaptation measures with current regulations, practices, and other adaptation measures (non-exhaustive list) resulting from the references cited in the sections 7.5.1 to 7.5.4 and from the authors' personal experience.

	Forestry	Agriculture	Water	Nature conservation
Forestry			Intensification of wood production (e.g. tree species choice) results in higher water use and reduced ground water levels	Non-native species (e.g. Douglas-fir)
Agriculture			Water use for irrigation reduces river discharge	
Water		Water retention in landscape and reservoirs reduces water availability for irrigation		Water reservoirs and raise and reallocation of dikes impact riparian ecology
Nature conservation	Larger 'wilderness' areas and reduced management intensity constrain wood production More structural diversity and importance of deadwood constrain forest management	Embedding more structural landscape elements in the agricultural landscape and connecting protected areas constrain production Reduction of landscape drainage/re-wetting leads to production losses	Rewetting of bogs and fens reduces river discharge	

Table 7-3 Possible synergies of adaptation measures with current regulations, practices, and other adaptation measures (non-exhaustive list) resulting from the references cited in the sections 7.5.1 to 7.5.4 and from the authors' personal experience.

	Forestry	Agriculture	Water	Nature conservation
Forestry			Forest conversion enhances water balance	Forest conversion increases biodiversity
Agriculture			Drought-adapted crop species enhance water balance	
Water	Water retention in landscape (e.g. rewetting, reduced drainage) mitigate drought and desiccation	Water retention in landscape (e.g. rewetting, reduced drainage) and reservoir management mitigate drought and desiccation		Water-retention benefits bogs, fens and wetlands
Nature conservation	Structural diversity leads to higher resilience, improved forest health and a diversification of (financial) risks	Organic farming reduces costs for fertilizer while increasing marketing opportunities	Bog rewetting and restoration improves regional water balance	

7.7 Adaptation of the 'Brandenburg system'

Past and future climatic changes and their impacts in each individual sector in Brandenburg can be interpreted as 'non-routine' climate variability and impacts defined by Dovers (2009) as "significantly exacerbated degree of variability and related impacts […] not outside the historical human experience" to which adaptation is possible. However, Nelson (2010) points out that the ability to adapt emerges from relationships within a system (the relationship in between sectors and also the influence of the socioeconomic situation in our case).Thus, if adaptation strategies in different fields are not compatible and lead to conflicts between sectoral adaptation activities and stakeholder groups, this hampers their successful implementation. The interaction of adaptation measures between individual sectors constrain the coping range of Brandenburg as a system beyond of what an analysis of each sectors' individual coping range would suggest (Smit & Wandel 2006). Adapting intensive agricultural production through irrigation conflicts with adaptation to high flow situations through increasing water retention in the landscape. Furthermore, stakeholders with different interests and values may oppose or favor certain adaptation options. Whereas private forest owners may consider Douglas-fir as an appropriate adaptation option and object to structured multi-species stands, the opposite may be true for nature conservationists. Individually, each measure seems to be a valid adaptation option, but at higher organizational levels, their implementation is contested and therefore restricted.

Furthermore, present and future socioeconomic conditions including cultural values can determine a system's vulnerability to a larger extent than climate change and undermine its resilience (Burton et al. 2002; Redman & Kinzig 2003). If the socioeconomic situation or the infrastructure in an area do not allow for water-retention measures in the landscape (e.g. because this is fertile agricultural land or an important traffic intersection), expensive flood protection will have to be built. Similarly, static nature conservation concepts shaped by a long history of nature protection in the absence of needing more dynamic approaches in view of changing conditions determine how protected areas are managed even when conditions are now more in flux. Furthermore, the availability of a skilled work force constrains the successful implementation of adaptation measures if these require better technical knowledge than conventional measures. A climate change-adapted forest management unit with several tree species may require more complicated silvicultural systems and planning than a conventional Scots pine monoculture. However, Wechsung et al. (2008) also found that climate change-induced yield losses on agricultural lands may be compensated by increasing prices.

Most of these issues are strongly dependent on the demographic development in Brandenburg which continues to face substantial challenges (see section 7.4). Although adaptation measures are available, mainstreaming, information of and communication with relevant stakeholders and the public, planning, financing, demographic development, and employment as well as current practices, laws, values, and administrative practices remain important barriers to their implementation. Such barriers may be more easily resolved if strong and visible impacts with immediate implications for society occur (e.g. in the water sector through floods) since these receive high public attention and make resources available (Adger et al. 2007). However, such events also distract public opinion and funding from effective adaptation (Adger et al. 2007) and thereby increase the risk of ignoring slowly changing variables which take an important part in shaping system dynamics (Carpenter & Turner 2001). A slowly decreasing water availability has strong impact on the productivity of forests and agricultural land but if no 'obvious' drought damage occurs, these effects are hard to quantify and it is difficult to receive support for adaptation. Such changes become, however, increasingly important if not only climate change impacts are considered but also the wider framework of global change, competition for resources and limited funding and its cascading impacts on social-ecological systems. Moreover, we only highlighted here the most prominent socioeconomic challenges that pertain to the whole region. Locally, the situation may be even more complicated which further hampers adaptation and exacerbates global change impacts.

Thus, although our review of current and planned adaptation measures shows that adaptation in each sectors seems feasible (see section 7.5), this may not be the case at the Brandenburg level. The conflicts outlined in section 7.6 support this view and emphasize that cross-sectoral approaches are necessary, especially in water management. Our analysis shows that even in a 'developed country' like Brandenburg successful adaptation at the regional level requires more efforts than perceived by individual actors, which challenges common perceptions of developed countries to "adapt when necessary" (Burton et al. 2002). Therefore, 'no/low regret' activities that foster climate change adaptation but also entail non-climatic benefits and reduce vulnerability (such as rewetting bogs to restore natural habitats) represent a crucial added value for climate change adaptation and may help to overcome implementation barriers (e.g. by providing new funding possibilities) (Smit & Wandel 2006; Klein et al. 2005; Dovers 2009). A recent study on adaptation in the United Kingdom came to the conclusion that non-climatic aspects drive adaptation activities currently carried out and that these often have significant cobenefits (Tompkins et al. 2010).

These points highlight the importance of focusing on the adaptation of Brandenburg as a system of nested subsystems that are strongly interdependent. This also allows benefiting from the synergies we identified that emerge from the interplay of adaptation measures in different sectors. Moreover, a more systemic perspective is a first step to avoid externalities of adaptation measures that increase a system's vulnerability (Turner et al. 2010, Adger et al. 2007). This implies that although local site conditions determine adaptation measures, adaptation has to occur at the landscape level and in an integrated manner (Heinimann 2010). Such an approach to climate change adaptation has strong linkages with sustainable development.

7.8 Implications for sustainable regional development

7.8.1 Linking adaptation and sustainable regional development

The basic linkages between climate change and development are clear: climate change results from socioeconomic development which in turn determines the vulnerability to climate change and the adaptive capacity of societies (Klein et al. 2005). Integrating climate change adaptation into broader policy processes such as sustainable development is known as 'mainstreaming' and its high importance is one of the main conclusions of the IPCC Fourth Assessment Report's chapter on adaptation (Adger et al. 2007) as well as of more recent development studies (e.g. Munasinghe 2010). Smit & Wandel (2006) argue that adaptation is more likely to be successful in the long-run if combined with sustainable development. More concretely, one recent line of research on climate change adaptation policies and development argues that for adaptation to be successful, it should focus on reducing vulnerability by increasing adaptive capacity rather than adjusting to the impacts of climate change alone (Burton et al. 2002; Schipper 2004, 2007; Klein et al. 2005). Adaptation strategies detached from development considerations will only partly be able to address the different levels and facets of vulnerability. The large range of impacts of global change that occur in ecological systems but that have an immediate connection to the vulnerability of social systems underline this mismatch. Adaptation as such will not lead to efficient and equitable development and therefore not respond to the aspirations of societies. These can only be fulfilled if adaptation is embedded in a larger sustainable development context, which implies that sustainable development is the priority and then adaptation a logical consequence (Schipper 2007). The importance of a systemic, holarchical view (cf. section 7.7) provides evidence that adaptation should be fully integrated into regional sustainable

development policies (and not only into sectoral development) to mediate conflicts and synergies between sectors and to reconcile comprehensive strategies with local realities (Fig. 7-5). The position paper on sustainable development of the federal state government of Brandenburg highlights the importance of further developing adaptation strategies and considering them in the sustainable development strategy which should be published until 2014 (MUGV 2011). A full integration of adaptation and sustainable development as well as links with vulnerability reduction is, however, not envisioned. For Brandenburg, which is part of one of the richest countries in the world but faces substantial socioeconomic problems combined with strong climatic impacts, these are pivotal conclusions. They entail far-reaching transformations of management processes and practices, a rethinking of how to combine and integrate sectoral adaptation measures and development policies, and a reconciliation of conflicting time- and spatial scales of adaptation and development priorities to create a resilient social-ecological system. This would also facilitate the integration of other strongly debated issues such as coupling Brandenburg's biomass strategy (MUGV 2010) with a larger land-use concept as proposed by the 'Council on Sustainable Development and Resource Protection' (Council on Sustainable Development and Resource Protection, unpublished).

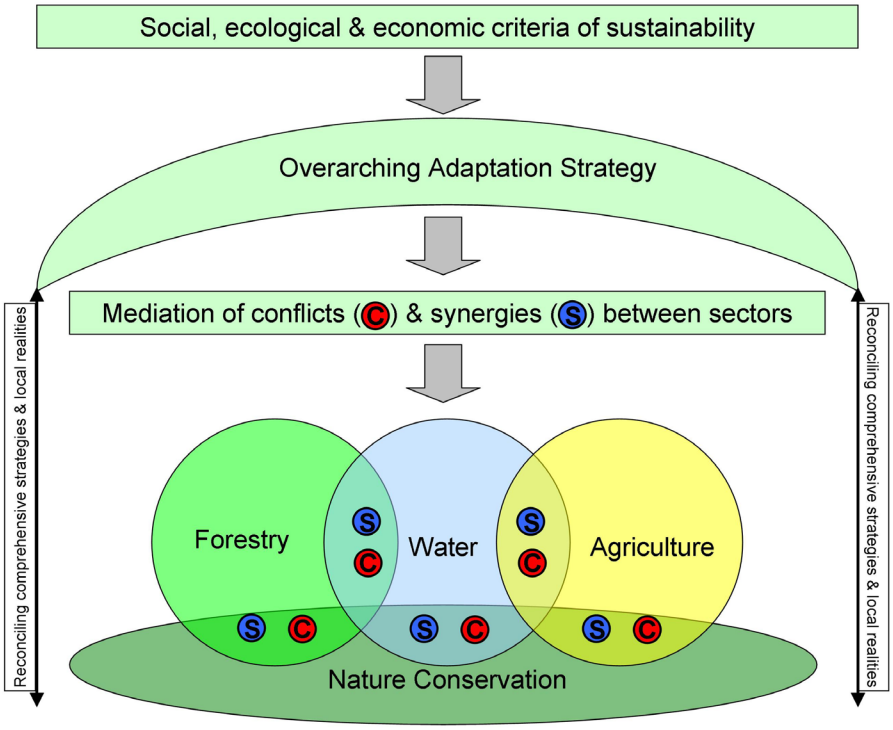

Fig. 7-5 Conceptualization of the integration of an overarching adaptation strategy into a broader context of sustainability. The overarching adaptation strategy supports the mediation of conflicts and synergies between sectors and strives to reconcile local realities with comprehensive, higher order strategic issues. The sectors are consistent with those addressed in the text but could be other sectors as well. It is noted that nature conservation is not a sector per se but rather happens in all of the other three sectors.

7.8.2 Adaptation and development for resilient social-ecological systems

Linking adaptation and sustainability as described above points toward building resilience since resilience is the concept for understanding and managing change in social-ecological systems (Folke 2006). A systemic perspective such as presented here which takes into account multiple drivers of change (e.g. climate change, unemployment), different actors (e.g. forest owners, farmers, nature conservationist, and tourists), and possible feedbacks (e.g. forest conversion provides deciduous wood to forest industry which in turn support further forest conversion) enhances resilience (Nelson 2010). Moreover, the "resilience of a system is not fixed but changes in line with changes in internal and external conditions" as Nelson (2010) puts it, which is crucial for both adaptation and sustainable development in times of changing environmental and socio-economic conditions and evolving values. Resilient systems may benefit from change and disturbances to transform into new states (Folke et al. 2005). Transformation into new states may be an adaptation option when 'conventional' adaptation options become limited (Nelson 2010). However, when changes are less disruptive, resilience is the basis for making use of opportunities arising from climate change.

In practice, resilience requires novel learning techniques (Tschakert & Dietrich 2010), adaptive governance (Folke et al. 2005) and adaptive management to cope with uncertain climatic and socioeconomic conditions and conflicting user groups across different spatial, temporal and organizational scales. A case study by Tompkins & Adger (2004) concluded that adaptive and community-based management enhances resilience through building of networks and maintaining the resilience of ecological systems. Adaptive management also highlights the importance of participation. Participation of stakeholders, actors but also the civil society in general as well as cooperation with government agencies is crucial for adaptation and sustainable development since many limits to adaptation and sustainable development are social ones, people are more likely to act if they perceive adaptation being within their powers, and successful adaptation depends to a large extent on values, belief in scientific findings, and ethics (Adger 2003; Lorenzoni & Hulme 2009; Adger et al. 2009; Bohunovsky et al. 2011; Otto-Banaszak et al. 2011). The choice of appropriate methods for engaging local people and stakeholders in adaptation dialogues depends on the specific objectives of the exercise. These objectives may include identifying research questions, collecting data and knowledge, creative search for adaptation and development options, prioritizing adaptation and development options or the use of limited funds, or resolving

conflicts. Small and large group methods such as Focus Groups (Welp et al. 2009a) or World Café (Hoffmann et al. 2011) have been tested successfully in pilot projects, which aimed at identifying priorities, responsibilities as well as urgent research questions. In a recent series of stakeholder dialogues, the need for action resulting from climate change was discussed as well as approaches to adaptation strategies developed (Hoffmann et al. 2011). The methods for engaging different sectors and industries represented by associations and companies, ministries and authorities and by civil society and academia can be applied in regional settings in Brandenburg.

Participation is however not only needed in policy-making and management. Science needs to open also for an extended-peer community (Ravetz 2006). Regional climate adaptation efforts, in particular if seen in the context of sustainable development, need the support from science. The problems are typically not well-structured, characterized by great uncertainties and conflicts of interest (Ravetz 2006). The traditional scientific approach is likely to produce only punctual insights and sectoral expertise. Transition science (Brown et al. 2010) puts emphasis on engaging local people and stakeholder groups. So far people who want to participate are hampered by a lack of organization, expertise and a theory of their work. Integrating local knowledge, new perspectives on research questions is likely to work if people feel there is an urgent issue that affects them. How this new community and collective intelligence can take part in scientific inquire has been conceptually and methodologically discussed by Welp et al. (2006, 2009b).

The challenge for adaptation is that in both forestry and agriculture, for example, multiple actors make decisions concerning the use of their land resources, material input for the production, tree species and crops they choose. These actors base their decisions on different knowledge bases: individual knowledge (personal lived experience), local knowledge (shared community event), and specialized knowledge (Brown et al. 2010). A combination of and respect for these competing knowledge bases needs to be the basis for collective action. Promising avenues for linking lay knowledge and scientific knowledge are provided by combining communication tools (dialogue methods) and analytical tools (Bayesian belief networks, system dynamic modeling) (Welp et al. 2006).

Thus, participation can help to avoid conflicts, to benefit from synergies and thus to combine and integrate sectoral adaptation and development approaches. Reconciling different and partly conflicting spatial and temporal scales of adaptation and development priorities deserve special emphasis in this process as well as in policy-making. In such an adaptive management framework, even imperfect vulnerability assessments (due to e.g. the

predictive uncertainty of climate and climate impact models (Burton et al. 2002)) help to point out where and who the most sensitive and exposed areas and groups are. This information can then steer sustainable regional development including adaptation. In practice, this may result in connected and diverse landscapes of forests, extensively used agricultural land, and waterways which are appealing to locals and tourists and provide multifunctional ecosystem services while supporting local livelihoods (which is not to downplay the possibility that even with focused, well-directed efforts, environmental degradation could be an outcome; but this would certainly be lessened as far as possible).

7.9 Conclusion and outlook

Here we provide a regional application of Burton et al. (2002)'s adaptation framework highlighting examples of synergies and conflicts between adaptation measures and linkages to development as requested by the IPCC's Fourth Assessment Report (Adger et al. 2007). We present a first attempt to move not only from an impact to a vulnerability assessment (Burton at al. 2002) but also from a sectoral to a systemic perspective of adaptation in the framework of sustainable development to create resilient social-ecological systems. Next steps toward successful adaptation would be a thorough, systematic analysis of barriers to climate change adaptation (especially social and cultural ones) following e.g. Moser & Ekstrom (2010)'s framework, a more detailed analysis of adaptation measures to current climatic variability (even though not termed adaptation, Burton et al. 2002)) to learn from existing experience but also the assessment of possible adaptation measures and their repercussions on the sustainable development of the entire 'system Brandenburg' (i.e., also those sectors not or only marginally covered here). Finally, linking the regional analysis at the level of Brandenburg to larger (national and international adaptation and development issues) to avoid and solve conflicts between these different organizational levels is necessary (Smit & Wandel 2006).

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8 Summary and conclusion

The model chains that are used to study the impacts of environmental change on forest ecosystem lead to a cascade of uncertainties. This thesis examines different types of uncertainties in modeling forest ecosystem responses to environmental change. The chapters 2-6 of this thesis address different aspects of the cascade of uncertainties and its implications for assessing forest productivity as an important ecological variable and a valuable ecosystem function for human societies. Chapter 7 has the character of an outlook chapter. It provides an overview of the broader framework in which the results of the preceding chapters have to be interpreted to enhance the sustainable management of natural resources and foster the sustainable development of rural regions.

The objective of chapter 2 is to provide a synthesis of process-based, stand-scale model predictions of changes in forest carbon and biomass pools and fluxes under climate change, elevated CO_2 and nitrogen deposition. This chapter shows that

- strong biases exist in terms of regions, drivers and forest types covered by stand-scale, process-based forest models.
- the effects of increasing CO_2 largely determine whether modeled responses to environmental change are positive or negative.
- the physiological response to climate change and increasing CO_2 increases until a warming of 0.4K per decade and declines thereafter.

These results reveal

- for which regions, drivers and forest types more detailed studies of the effects of environmental change on changes in forest carbon and biomass pools and fluxes are needed.
- that the CO_2-effect is a crucial model structural uncertainty across a large number of models.
- that a threshold of 0.4K warming per decade seems to be a physiological boundary beyond which productivity definitely declines in non-tropical forests even without taking into account changing disturbance regimes.

The objective of chapter 3 is to assess productivity shifts in Europe under various climate change scenarios and elevated CO_2 using the process-based forest model 4C. This chapter shows that

- a regional stratification in climate change impacts exists: mostly positive responses in boreal forests, mixed responses in central Europe and possibly negative effects in the Mediterranean.
- these results are partly overwhelmed by increasing levels of CO_2 and the positive effects on photosynthesis and water-use efficiency.

These results

- confirm and refine earlier results from European-wide assessments but advance the state of the art since they use one single stand-level, process-based model over Europe and detailed site, climate and stand information from forest monitoring plots.
- provide an important baseline for scenario studies of future timber availability but also for assessing changes in the carbon sequestration potential of forests and for developing adaptive forest management strategies.

The objective of chapter 4 is to integrate parameter uncertainty into simulations of climate change impacts on forest productivity using the process-based forest model 4C. This chapter shows that

- simulated changes in forest productivity induced by climate change and parameter uncertainty can be substantially higher than forest productivity changes induced by climate change alone.
- the direction of forest productivity change is mostly consistent between the simulations using the standard parameter setting of 4C and the majority of the simulations including parameter uncertainty.

These results highlight that

- climate change impact studies that do not integrate parameter uncertainty may over- or underestimate climate change impacts on forest ecosystems.

The objective of chapter 5 is to compare several European forest models before and after Bayesian calibration in four European countries and to quantify the uncertainty of their predictions. This chapter shows that

- Bayesian calibration reduces uncertainties strongly in all but the most complex model.

- Bayesian model comparison identifies 4C as the most plausible model after calibration among the six studied forest models.
- Bayesian model averaging is a robust way of predicting forest growth that accounts for both parametric and model structural uncertainty.

These results

- provide an easy introduction to the methodological approach for prospective users which is particularly valuable since current model studies usually do not consider model structural and parametric uncertainty.

The objective of chapter 6 is to review the effects of climatic variability on plants at different scales. This chapter shows that

- plant water relations are particularly vulnerable to changing climatic variability.
- interactions of physiological and phenological processes culminate in sophisticated responses to changing climatic variability at the species and community level.
- a combination of experimental, observational and modeling studies overcomes important caveats of the respective individual approaches.

These results

- stress that studies of climate change effects on plants focus much more on changing mean climate than on changing climatic variability. However, plants respond to extreme rather than to average conditions.
- guide and foster future experimental, observational and modeling studies and most importantly their integration.

The objective of chapter 7 is to provide an integrated analysis of climate change adaptation measures in agriculture, forestry, nature conservation and water management in a sustainable development framework. This chapter describes the wider framework in which the results of the preceding chapters have to be included to enhance the sustainable management of natural resources. It shows that

- there are synergies and conflicts between adaptation measures and linkages to regional development in Brandenburg.

- it is possible to move not only from an impact to a vulnerability assessment but also from a sectoral to a systemic perspective of adaptation in the framework of sustainable development to create resilient social-ecological systems.

These results emphasize

- the need for cross-sectoral, adaptive management practices that jointly target a sustainable regional development.

The results of the individual chapters are stand-alone scientific findings. However, the main objective of this thesis is to address the cascade of uncertainty in environmental change studies in a structured way at the example of forest ecosystems. This can only be achieved by synthesizing the findings of the individual chapters. Therefore, besides the more specific research gaps addressed in the individual chapters, I endeavor to tackle a broader research challenge: There are many valuable studies that address individual components of the cascade of uncertainty but this thesis is a hitherto unmatched effort to identify which aspects of uncertainty need to be considered in the cascade of uncertainties and to assess their importance in modeling forest ecosystem responses to environmental change. I achieve this by means of quantitative modeling as well as qualitative, conceptual work and I apply the theoretical framework of the cascade of uncertainties to assess if findings of changing forest productivity under environmental change are robust despite various uncertainties.

This thesis highlights that some impacts of environmental change on forest ecosystems are already well-captured by current models. This increases the confidence that ongoing climate change will cause physiological changes in forest productivity that are likely to be positive in non-water-limited forests while being rather negative in water-limited forests. However, changing disturbance regimes and extreme climatic events may also strongly affect forest productivity and this is not well-covered by the models considered in this study. Besides the, partly very specific, results found in the chapters 2-6, this thesis also shows how addressing environmental change fits into a broader sustainable development context in nested systems of coupled social-ecological systems (‘Panarchies’ sensu Gunderson & Holling 2002). It does so at the example of adaptation to climate change in several natural resource systems in the framework of regional sustainable development in the Brandenburg region in Germany.

The synthesis of the different chapters of this thesis also leads to the conclusion that, thus far, the cascade of uncertainties in modeling forest ecosystem responses to environmental

change is a great challenge for sustainable resource management if decision-makers are not made aware of existing uncertainties. Therefore, this thesis shows that a more systematic treatment of uncertainties, especially in the context of a cascade of uncertainties, is strongly needed to identify projections of the impacts of environmental change on natural resource systems that are robust despite existing uncertainties. These robust projections are the backbone of sustainable management since they provide a science-based decision space to policy-makers and managers and not only one normative, technocratic prescription. Thus, decision-makers can explore a variety of options that fit the broader societal context. Therefore, considering uncertainties in models should not only focus on a specific location of uncertainties such as the model parameters but rather on the whole spectrum of input, parameter and structural uncertainties. This can be done for example by considering ensembles of climate change scenarios as model input, by integrating parameter uncertainty through Monte-Carlo simulations and by carrying out model intercomparisons that account for different model structures. Data assimilation techniques such as Bayesian calibration or Bayesian model comparison are very valuable for these analyses.

The findings of this thesis provide an overarching framework in which both modelers as well as decision-makers that are to be informed by modeling studies can integrate model results and assess their robustness and probability. This framework can be applied to all kinds of model chains. By showing how individual model studies address parts of the cascade of uncertainty and by highlighting which types of uncertainty they address, this work ultimately contributes to science-based adaptive management and learning that are an integral part of the transformation toward resilient and sustainable social-ecological systems.

To increase the confidence of decision-makers and practitioners in scientific assessments future studies should strive to assess which scientific findings are robust or at least highly probable despite existing uncertainties. This could be paralled by research on how to better communicate uncertainties to decision-makers and practitioners or more concretely how to make use of participative methods to better communicate uncertainties and how to train decision-makers in probabilistic thinking. This also includes to move forward from showing uncertainties of scientific findings to providing science-based assessments of the available decision space as well as a more advanced treatment of the cascade of uncertainties for example a combination of bottom-up and top-down assessments of uncertainties. By starting from both ends of the cascade of uncertainties researchers and stakeholders could identify which uncertainties are already well-captured by current decision-making, which can

be easily assessed in scientific studies and most importantly which are not or only seldom addressed in scientific studies but crucial for decision-making.

Finally, the concept of the cascade of uncertainties is not only relevant for decision-making but also for science and particularly sustainability science per se. Addressing the different locations of uncertainty can lead to model development and improved understanding of processes and system dynamics. For example, future studies on forest productivity under environmental change may focus on establishing a sound understanding of the interaction of changing forest productivity with changing disturbance regimes and extreme events which is crucial for understanding the effects of environmental change on the carbon cycle and on forest resources. A better integration of changing societal preferences and needs into modeling efforts and unraveling the couplings of natural and social systems from different disciplinary and interdisciplinary perspectives would improve the understanding and ability to manage social-ecological systems under uncertainty. This could be done in small steps such as synthesizing existing material from different sources and disciplines to lay the foundation for large integrated frameworks, where experimental, observational and modeling studies are combined across disciplines and the different types of uncertainties are systematically addressed at each step of the cascade of uncertainty.

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9 Appendix

9.1 Appendix to chapter 1

Explanation of Representative Concentration Pathways (RCPs)

Recently, the SRES scenarios have been replaced by so-called Representative Concentration Pathways (RCPs) for the Fifth Assessment Report of the IPCC (Moss et al. 2010; van Vuuren et al. 2011). In this new approach, the socioeconomic scenarios have been decoupled from the climate forcing. Instead, a broad range of concentration pathways is being covered by four different RCPs which also rely on IAMs and subsequent downscaling of land-use and emission data and processing with simple carbon cycle and atmospheric chemistry models. However, the assumptions underlying the IAMs are not new socioeconomic scenarios anymore but in parallel, new socioeconomic scenarios (SSPs) are being developed that match the RCPs. This allows for a broader range of socioeconomic scenarios. This development does however only slightly change the flow of information and uncertainty displayed in the cascade of uncertainties (Fig. 1-2).

9.2 Appendix to chapter 3

Model 4C

The model 4C ('FORESEE' - FORESt Ecosystems in a changing Environment) has been developed to investigate long-term forest behavior under changing environmental conditions (Bugmann et al. 1997; Schaber et al. 1999; Fontes et al. 2010). It describes processes on tree and stand levels based on findings from eco-physiological experiments (e.g. Medlyn & Jarvis 1999), investigations of tree growth and architecture (e.g. Burger 1948), long-term observations of stand development and physiological modeling (e.g. Haxeltine & Prentice 1996). 4C simulates forest growth and structure, leaf area index, as well as ecosystem carbon and water balances. Establishment, growth and mortality of tree cohorts are explicitly modeled on individual patches on which horizontal homogeneity is assumed. The start and end of the vegetation period are estimated as functions of air temperature and day length (Schaber & Badeck 2003). The annual course of net photosynthesis is simulated with a mechanistic formulation of net photosynthesis as a function of environmental influences (temperature, water and nitrogen availability, radiation, and CO_2) where the physiological capacity (maximal carboxylation rate) is calculated based on optimization theory (modified after Haxeltine & Prentice (1996)) plus calculation of total tree respiration following the concept of constant annual respiration fraction as proposed by Landsberg & Waring (1997). The allocation pattern of annual net primary productivity (NPP) to the tree organs and tree growth are modeled with a combination of pipe model theory (Shinozaki et al. 1964a), the functional balance hypothesis (Davidson 1969), and ideas presented by Mäkelä (1990), with a number of corrections and modifications to make the model sensitive to changing environmental conditions. Establishment and mortality are described based on the concepts proposed by Keane et al. (1996), Loehle & LeBlanc (1996) and Sykes & Prentice (1996). Mortality can be caused either by stress due to negative leaf mass increment in successive stress years or by an intrinsic age-dependent and generic component. The tree cohorts' competition for water and nutrients is modeled via absorption of water and nitrogen by the fine roots in proportion to the fine root mass of the individual cohorts in the soil layers. Potential evapotranspiration is calculated in this 4C version according to Turc/ Ivanov (Dyck & Peschke 1995).

The soil model of 4C consists of a water, temperature, and carbon/nitrogen sub-model. The soil is divided into layers of varying thickness according to the soil horizons (organic layer and mineral soil horizons). The physical and chemical soil parameters and the initial carbon and nitrogen stocks as sum of soil organic matter and dead organic matter (litter) are derived from measurements or from soil maps. Water content, soil temperature, carbon, and nitrogen content of each layer are estimated as functions of the basic soil parameters, air temperature, net precipitation, and N deposition beneath the canopy. The carbon and nitrogen dynamics are driven by the litter input which is separated into five fractions for each species type (stems, twigs and branches, foliage, fine roots and coarse roots). The turnover of all litter fractions and of the soil organic matter compartment is described as a first order reaction (Grote et al. 1999). These processes are controlled by matter- and species-specific reaction coefficients and modified by soil moisture, temperature and pH value.

Different time steps are used for the various submodels, ranging from a daily time step for soil water dynamics, heat balance, soil carbon, and nitrogen dynamics, over a weekly time step for the simulation of NPP, to an annual time step for tree demography and carbon allocation. 4C allows the simulation of management of mono- and mixed species forests. For this purpose, a variety of thinning, harvesting and regeneration strategies are implemented.

It has been used to simulate impacts of global change in the forest sector in Germany (Lasch et al. 2002) or regional water balances and carbon storage in Brandenburg, Germany (Suckow et al. 2002; Gerstengarbe et al. 2003; Lasch et al. 2005). Furthermore, 4C has been validated using measurements of soil temperature and soil water content at Level-II sites in Germany (Badeck et al. 2007; Meiwes et al. 2007). The performance of 4C in comparison with other models against long-term data from Scots pine stands in Finland was investigated using volume growth and survival graphs (Mäkelä et al. 2000; Sievänen et al. 2000). Moreover, 4C was evaluated together with other process-based forest models and applied on the scale of a management unit to develop adaptive management measures and to compare different forest functions (Kellomäki & Leinonen 2005; Fürstenau et al. 2007; Fürstenau 2008). Further applications concern the analysis of forest conversion management (Kint et al. 2009), competition in mixed-forests (Reyer et al. 2010), alternative forest management strategies (Gutsch et al. 2011) or the analysis of short-rotation coppices (Kollas et al. 2009; Lasch et al. 2010) under climate change.

Stand data

This study depends on the plot selection. The Level-II plots are not representative of European forest conditions in a statistical sense. However, the Level-II plots are forests stands selected by experts in each country that are typical for that country and hence do represent the growing conditions and stand history of Europe's forests. From the larger subset of Level-II stands, we selected a smaller (but still comparably large) subset for this study according to the criteria and steps shown in Fig. 9-1.

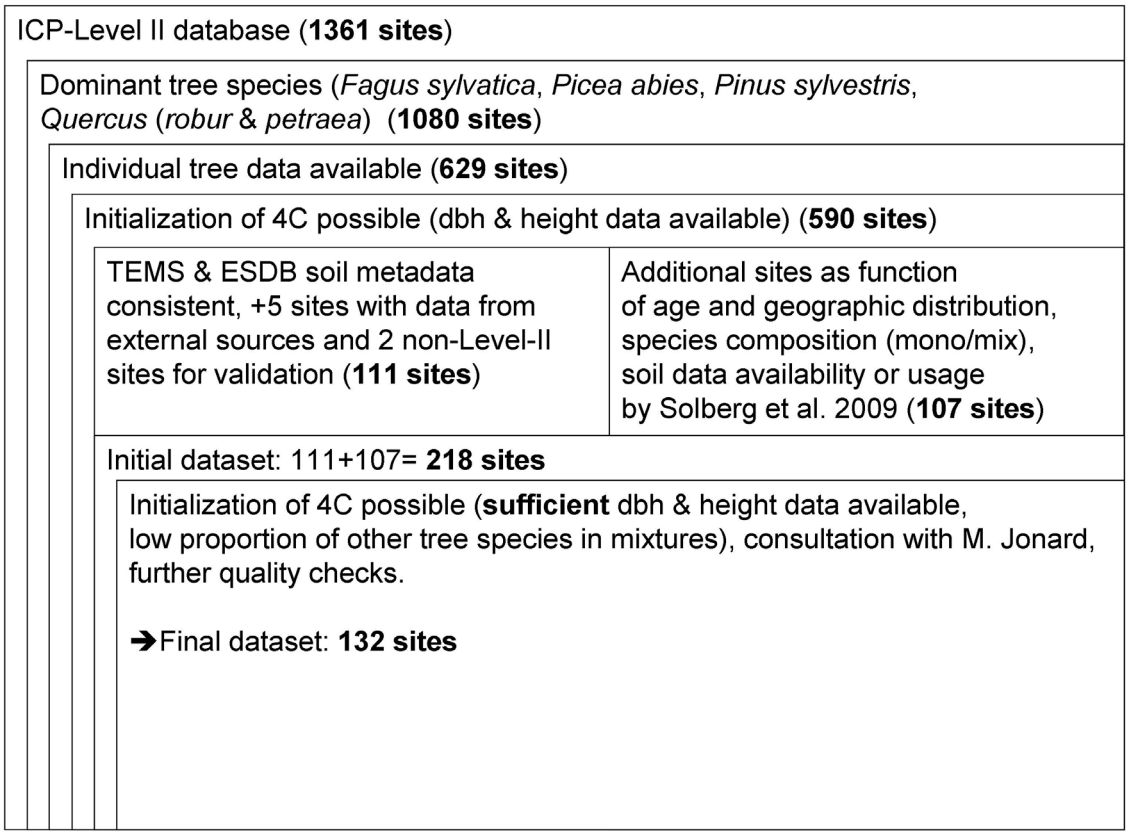

Fig. 9-1 Steps of plot selection carried out in this study (dbh = diameter at breast height).

Table 9-1 Plot locations, altitude (m above sea level), age class, main tree species, country and environmental zone after Metzger et al. (2005).

ID	Lat.	Long.	Altitude	Age	Main species	Country	Environmental Zone**
AU11	47.88	13.35	825	>120	*Picea abies*	Austria	CON
AU6	48.36	15.21	875	81-100	*Picea abies*	Austria	CON
AU9	48.12	16.05	525	41-60	*Fagus sylvatica*	Austria	CON
BL1	49.96	4.83	475	41-60	*Picea abies*	Belgium	CON
BL15	51.31	4.52	16	41-60	*Pinus sylvestris*	Belgium	ATC
BL17	51.00	4.21	25	>120	*Fagus sylvatica*	Belgium	ATC
BL2	50.23	5.62	575	41-60	*Picea abies*	Belgium	CON
BL21	50.75	4.41	125	81-100	*Fagus sylvatica*	Belgium	ATC
BL3	49.77	5.46	425	41-60	*Picea abies*	Belgium	CON
BL4	50.24	5.99	575	61-80	*Picea abies*	Belgium	CON
BL5	50.59	6.11	425	61-80	*Fagus sylvatica*	Belgium	CON
BL6	50.05	5.22	425	61-80	*Fagus sylvatica*	Belgium	CON
CZ2029	50.56	15.96	525	41-60	*Picea abies*	Czech Republic	ALS
DL101	54.10	10.24	25	81-100	*Fagus sylvatica*	Germany	ATN
DL1201	53.10	12.43	75	61-80	*Pinus sylvestris*	Germany	CON
DL1205	51.80	13.56	75	61-80	*Pinus sylvestris*	Germany	CON
DL1404	51.12	14.55	425	81-100	*Picea abies*	Germany	CON
DL1602	50.61	10.77	825	81-100	*Fagus sylvatica*	Germany	ALS
DL201	53.46	9.88	75	41-60	*Pinus sylvestris*	Germany	ATN
DL202	53.45	9.91	75	>120	*Quercus petraea*	Germany	ATN
DL301	52.84	10.28	125	101-120	*Fagus sylvatica*	Germany	ATN
DL303	51.86	10.42	675	41-60	*Picea abies*	Germany	ALS
DL304	51.76	9.58	500	>120	*Fagus sylvatica*	Germany	ATN
DL305	51.77	9.58	500	101-120	*Picea abies*	Germany	ATN
DL307	52.91	7.86	25	41-60	*Pinus sylvestris*	Germany	ATN
DL503	51.69	7.26	75	101-120	*Fagus sylvatica*	Germany	ATC
DL602	50.43	9.68	425	61-80	*Fagus sylvatica*	Germany	CON
DL604	50.16	9.38	425	>120	*Fagus sylvatica*	Germany	CON
DL701	49.70	7.03	625	61-80	*Picea abies*	Germany	ATN
DL702	50.43	7.09	575	81-100	*Picea abies*	Germany	ATN
DL703	49.63	7.92	575	61-80	*Fagus sylvatica*	Germany	CON
DL704	50.41	7.73	375	101-120	*Fagus sylvatica*	Germany	ATN
DL705	49.27	7.81	525	>120	*Quercus petraea*	Germany	ATC
DL706	49.02	8.13	125	81-100	*Quercus robur*	Germany	PAN
DL707	49.31	7.87	525	>120	*Pinus sylvestris*	Germany	ATC
DL805	47.78	7.71	1025	101-120	*Picea abies*	Germany	CON
DL914	49.98	9.46	475	81-100	*Quercus petraea*	Germany	CON
DL915	47.88	10.80	775	61-80	*Fagus sylvatica*	Germany	CON
DL916	47.57	10.39	1175	101-120	*Picea abies*	Germany	CON
DL919	48.41	11.66	525	>120	*Fagus sylvatica*	Germany	CON
DL920	50.47	11.35	675	61-80	*Picea abies*	Germany	CON
EE2	59.58	26.13	25	41-60	*Pinus sylvestris*	Estonia	NEM
EE6	58.36	26.98	75	41-60	*Picea abies*	Estonia	BOR
ES13	43.16	-5.48	775	61-80	*Quercus robur*	Spain	LUS
ES3	42.26	-2.70	1275	61-80	*Fagus sylvatica*	Spain	MDM
ES47	42.30	1.88	1525	61-80	*Pinus sylvestris*	Spain	MDM
ES5	40.87	-3.97	1625	101-120	*Pinus sylvestris*	Spain	MDM
FR15	49.37	1.50	175	61-80	*Quercus petraea*	France	ATC
FR25	47.80	0.38	175	81-100	*Quercus petraea*	France	ATC
FR3	43.74	-0.84	25	41-60	*Quercus robur*	France	LUS
FR41	45.76	2.97	925	21-40	*Picea abies*	France	ALS
FR49	46.19	3.00	575	61-80	*Fagus sylvatica*	France	ATC
FR51	42.93	1.28	1225	101-120	*Fagus sylvatica*	France	MDM
FR52	49.18	-0.86	75	61-80	*Fagus sylvatica*	France	ATC
FR62	49.32	2.88	125	41-60	*Fagus sylvatica*	France	ATC
FR65	49.71	1.33	225	61-80	*Fagus sylvatica*	France	ATC
FR67	48.11	6.25	375	41-60	*Fagus sylvatica*	France	ATC
FR76	44.03	6.67	1675	61-80	*Pinus sylvestris*	France	MDM
FR80	47.54	-1.80	25	41-60	*Pinus sylvestris*	France	LUS
FR86	49.45	0.75	75	41-60	*Pinus sylvestris*	France	ATC
FR87	48.69	1.73	175	41-60	*Pinus sylvestris*	France	ATC
HU2	47.89	19.95	575	41-60	*Picea abies*	Hungary	PAN
IT1	41.85	13.59	1564	101-120	*Fagus sylvatica*	Italy	MDM
IT20	46.06	12.03	1075	101-120	*Fagus sylvatica*	Italy	MDM
LT9	55.80	25.53	125	41-60	*Picea abies*	Lithuania	NEM
NL174	51.33	5.52	25	41-60	*Pinus sylvestris*	The Netherlands	ATC
NL226	51.55	4.77	25	41-60	*Quercus robur*	The Netherlands	ATC
NO15	63.29	11.18	275	>120	*Picea abies*	Norway	ALN
NO17	69.00	19.43	175	41-60	*Picea abies*	Norway	ALN
NO18	62.78	8.89	275	101-120	*Pinus sylvestris*	Norway	ALN
NO4	65.88	13.80	375	>120	*Picea abies*	Norway	ALN
NO5	69.45	30.04	25	61-80	*Pinus sylvestris*	Norway	BOR

ID	Lat.	Long.	Altitude	Age	Main species	Country	Environmental Zone**
NO6	58.98	11.53	125	81-100	*Picea abies*	Norway	NEM
NO9	59.45	9.87	175	101-120	*Picea abies*	Norway	BOR
PL1	52.37	19.90	125	61-80	*Pinus sylvestris*	Poland	CON
PL11	52.00	17.33	125	61-80	*Pinus sylvestris*	Poland	CON
PL124	50.61	17.69	175	61-80	*Fagus sylvatica*	Poland	CON
PL125	50.31	18.48	225	41-60	*Fagus sylvatica*	Poland	CON
PL130	49.87	22.61	325	61-80	*Quercus robur*	Poland	CON
PL137	53.98	19.43	125	61-80	*Fagus sylvatica*	Poland	CON
PL141	52.75	14.87	75	61-80	*Fagus sylvatica*	Poland	CON
PL150	49.61	19.09	725	41-60	*Picea abies*	Poland	CON
PL19	52.53	14.95	25	41-60	*Pinus sylvestris*	Poland	CON
PL28	53.81	16.36	75	41-60	*Pinus sylvestris*	Poland	CON
PL30	54.20	17.23	125	61-80	*Pinus sylvestris*	Poland	CON
PL31	54.16	17.12	125	41-60	*Pinus sylvestris*	Poland	CON
PL38	52.85	23.68	125	41-60	*Pinus sylvestris*	Poland	NEM
PL40	53.29	22.05	125	41-60	*Pinus sylvestris*	Poland	CON
PL51	53.65	20.19	125	41-60	*Pinus sylvestris*	Poland	CON
PL55	53.96	18.12	175	41-60	*Pinus sylvestris*	Poland	CON
PL61	53.82	17.85	125	61-80	*Pinus sylvestris*	Poland	CON
PL68	50.43	17.96	175	41-60	*Pinus sylvestris*	Poland	CON
PL75	51.37	15.68	175	41-60	*Pinus sylvestris*	Poland	CON
RO10	47.45	25.56	1375	61-80	*Picea abies*	Romania	ALS
SF1	69.58	28.90	125	>120	*Pinus sylvestris*	Finland	BOR
SF10	61.87	24.20	175	61-80	*Pinus sylvestris*	Finland	BOR
SF11	61.85	24.31	175	61-80	*Picea abies*	Finland	BOR
SF17	61.81	29.32	75	61-80	*Picea abies*	Finland	BOR
SF2	67.95	24.06	325	81-100	*Pinus sylvestris*	Finland	ALN
SF21	66.30	29.50	275	>120	*Picea abies*	Finland	BOR
SF24	62.47	21.53	25	41-60	*Picea abies*	Finland	BOR
SF26	61.93	23.33	175	81-100	*Pinus sylvestris*	Finland	BOR
SF3	68.00	24.24	275	>120	*Picea abies*	Finland	ALN
SF31	66.34	26.65	225	61-80	*Picea abies*	Finland	BOR
SF9	64.97	26.38	75	81-100	*Pinus sylvestris*	Finland	BOR
SR202	48.64	19.05	625	>120	*Fagus sylvatica*	Slovak Republic	CON
SR203	48.93	19.49	1225	41-60	*Picea abies*	Slovak Republic	CON
SW1114	56.18	13.15	75	41-60	*Pinus sylvestris*	Sweden	NEM
SW5401	58.95	16.98	25	61-80	*Picea abies*	Sweden	NEM
SW5503	58.98	15.86	75	61-80	*Picea abies*	Sweden	NEM
SW6011	56.32	15.71	75	81-100	*Quercus robur*	Sweden	CON
SW6103	56.13	13.51	125	41-60	*Picea abies*	Sweden	NEM
SW6108	56.18	14.25	125	21-40	*Picea abies*	Sweden	CON
SW6110	56.25	13.53	125	81-100	*Fagus sylvatica*	Sweden	NEM
SW6201	55.93	13.60	75	81-100	*Quercus robur*	Sweden	CON
SW6203	55.62	13.44	125	21-40	*Picea abies*	Sweden	CON
SW6301	57.08	12.55	75	61-80	*Fagus sylvatica*	Sweden	NEM
SW6302	56.95	12.72	75	41-60	*Picea abies*	Sweden	NEM
SW6303	56.78	13.15	175	21-40	*Picea abies*	Sweden	NEM
SW6305	57.01	13.38	175	61-80	*Picea abies*	Sweden	NEM
SW6308	57.21	12.47	75	81-100	*Quercus petraea*	Sweden	NEM
SW6309	57.04	12.80	175	81-100	*Fagus sylvatica*	Sweden	NEM
SW7001	61.12	14.36	275	41-60	*Pinus sylvestris*	Sweden	BOR
SW7004	61.20	15.20	225	41-60	*Pinus sylvestris*	Sweden	BOR
SW7202	63.17	17.93	175	81-100	*Pinus sylvestris*	Sweden	BOR
SW7301	62.00	14.43	375	81-100	*Pinus sylvestris*	Sweden	BOR
SW7402	64.50	18.47	275	61-80	*Pinus sylvestris*	Sweden	BOR
SZ13	47.40	8.23	475	>120	*Fagus sylvatica*	Switzerland	CON
SZ2	46.72	7.76	1525	>120	*Picea abies*	Switzerland	CON
SZ9	46.27	7.44	1075	>120	*Pinus sylvestris*	Switzerland	ALS
Hesse*	48.67	7.06	300	21-40	*Fagus sylvatica*	France	ATC
Hyytiälä*	61.85	24.30	170	21-40	*Pinus sylvestris*	Finland	BOR

*these stands are not part of the ICP Level-II database

**Environmental zones: Alpine North (ALN), Boreal (BOR), Nemoral (NEM), Atlantic North (ATN), Alpine South (ALS), Continental (CON), Atlantic Central (ATC), Pannonian (PAN), Lusitanian (LUS), Mediterranean Mountains (MDM)

Climate data: Explanation of the CCLM realizations

The realizations result from different initialization times of the GCM that drives CCLM: First, the GCM (in this case ECHAM5) has been run for a long time (~500 years) under constant CO_2 until ocean and atmosphere are in equilibrium. This is the so called pre-industrial control experiment. Then the GCM has been initialized from two different points of the pre-industrial control experiment to cover different points of the decadal climatic oscillation and

from each point it has been run for 100 years with the 20th century CO_2 and sulfur forcing. These runs are called 20th century reconstruction runs and are different realizations of the same greenhouse gas forcing. The end of each of the runs, i.e. the year 2000 of the different realizations, is then taken as a starting point for the scenario runs according to the greenhouse gas concentrations of the different SRES emission scenarios. This results in two different realizations of the same SRES emission scenario. The realizations with the same forcing should provide similar climates in the long term but can be quite different in the short-term due to their different starting point in the decadal oscillation. The past and corresponding future GCM runs are then used to drive CCLM and thus result in different RCM realizations. In this way, the different realizations account partly for the uncertainty in climate models.

Climate data: Bias correction

To account for biases in the RCMs, we carried out a bias-correction according to the following method. We calculated the difference (or ratio) of measured and simulated historic climate for every grid point (i.e. the model bias) and assumed that this bias will persist in future scenarios (e.g. if bias of measured and simulated past climate is 20% always deduce 20% from future climate). We calculated a monthly mean model bias in absolute terms for temperature and in relative terms for precipitation. This yields 12 values for period 1960-2000. We then added (in the case of temperature) or multiplied (in the case of precipitation) this bias to/with daily simulated climate of past and future to obtain final corrected time series. Every day of the simulated climate is corrected with a monthly correction factor (e.g. every daily value in January of every year is corrected with the same correction factor).

This method corrects the future with model bias of the past. The advantage of this method is that the individual climate variables still fit together. The corrected climate variables represent the conditions of those climate variables that will not be corrected for model bias; e.g. a rainy day remains rainy after correction and thus the corresponding global radiation, relative humidity etc. still represent the conditions of a rainy day.

Soil data: Additional information on the preparation of soil data from the ESD

In the ESD, several soil types may occur in each polygon (called soil map unit). Therefore, we linked this information with the soil information provided by the TEMS database (GTOS/TEMS 2011), which assigns a soil type to each Level-II plot. We then developed a simple algorithm to assign detailed soil data from the ESD to each Level-II plot based on the TEMS information. In the ESD, each polygon contains one or several soil types (called soil type units) which feature distinct soil profiles. To link this detailed soil profile description to a specific Level-II site, we checked whether the soil type provided by the TEMS database of a specific Level-II plot appeared in the respective ESD polygon in which this plot was located. In some cases the information of the TEMS database and the information of the ESD were identical and thus each Level-II site could be directly assigned a soil profile from the ESD. If this was not the case we proceeded as follows: If the soil information of the ESD and the TEMS database were not consistent but the main soil types (e.g. cambisol) were, we linked the Level-II plot to the dominant soil profile of that main soil type in this polygon. In all other cases (either no consistent main soil type or no information in the TEMS database), we linked the Level-II plot to the dominant soil profile in this polygon. This approach assumes that the Level-II plots which represent typical forests may also be located on the typical soils which are represented by the most dominant soil type in each polygon. Since the ESD does

not provide information on organic layers we estimated the carbon content from topsoil organic carbon content (0-25cm) and assumed a density of 0.2g cm^{-3}.

Validation

The main processes of 4C relevant for carbon and water fluxes were validated at nine climatically different sites using detailed measurement data from EUROFLUX and Level-II sites of ICP Forests. To assess the model's validity under past conditions we carried out a number of comparisons with observed data. The stand and soil data used for initializing the model run as well as the climate data as driving forces were based on observations at the validation site.

It is not recommended to validate a complex process-based model as 4C with one single output variable (see also Fontes et al. 2010); therefore, we validated as many processes as possible comparing different output variables that pertain to different model processes. We used carbon and water flux data measured on flux towers using eddy-covariance methods, soil temperatures and soil water content measures in different soil layers.

Validation Data

Nine sites with different species and site conditions for which enough detailed input data and data for model validation were available, were part of the 132 study sites. For model validation we ran the model with site-specific measured climate time series as far as available on these nine sites. This data was derived from the Level-II database and in the case of those plots that were not Level-II plots provided by the EUROFLUX network (Table 9-2) or the NORDFLUX project (P. Kolari, Pers. Comm. January 2011). The NORDFLUX data has been gap-filled using standard techniques (P. Kolari, Pers. Comm. January 2011).

Table 9-2 Data sources for the validation of 4C.

Site	Stand data	Soil data	Climate data	Observation data
Brasschaat	Cermak et al. 1998	FutMon 'Water Budget Model Comparison' (Personal Communication B. Klöcking, 2010), Website CarboEuropeIP (2002)		
Collelongo	Schulze 2000	Website European Ecosystem Database CarboEuropeIP 2011, Reichstein et al. 2005; Papale et al. 2006		
Hesse	Personal communication (FW Badeck, A. Granier, 2005)	Website CarboEuropeIP (2002)		
Hyytiälä	NORDFLUX project (Personal communication, P. Kolari, January 2011)			
DL1201	Level-II data base, ForestFocus (Badeck et al. 2007)			
DL1205	Level-II data base, ForestFocus (Badeck et al. 2007)			
DL 304	Level-II data base, ForestFocus (Badeck et al. 2007)			
DL 305	Level-II data base, ForestFocus (Badeck et al. 2007)			
DL919	Level-II data base, ForestFocus (Badeck et al. 2007)			

Validation criteria

For validation purposes, we compared simulated results (P_i) with observed data (O_i) where the subscript *i* indicates the time reference. There are many criteria to analyze the model quality (Medlyn et al. 2005, Krause et al. 2005). In this study four criteria were selected (Table 9-3) which allow for a comparison of the results irrespective of the absolute values of variables and their order of magnitude.

Table 9-3 Efficiency criteria used for the validation of 4C.

Code	Efficiency criteria	Formula[1)]
NMAE	Normalized mean absolute error	$\frac{\frac{1}{N}\sum_{i=1}^{N}\lvert P_i - O_i\rvert}{\bar{O}}$
NRMSE	Normalized root mean square error	$\frac{1}{\bar{O}}\sqrt{\frac{1}{N}\sum_{i=1}^{N}(P_i - O_i)^2}$
MEFF	Nash–Sutcliffe model efficiency coefficient[2)]	$1-\frac{\sum_{i=1}^{N}(O_i - P_i)^2}{\sum_{i=1}^{N}(O_i - \bar{O})^2}$
CC	Correlation coefficient	$\frac{\sum_{i=1}^{N}\left(O_i - \bar{O}\right)\left(P_i - \bar{P}\right)}{\sqrt{\sum_{i=1}^{N}\left(O_i - \bar{O}\right)^2\sum_{i=1}^{N}\left(P_i - \bar{P}\right)^2}}$

1) $\bar{O},\bar{P}$ are the mean of observed and simulated data respectively
2) Nash & Sutcliff (1970)

Another criterion is the direct comparison of observed versus simulated data in a scatter plot which can then be analyzed with a linear regression and the calculation of the coefficient of determination R^2, the intercept a and the slope b:

$$P_i = a + b\,O_i$$

$$R^2 = \left(\frac{\sum_{i=1}^{N}\left(O_i - \bar{O}\right)\left(P_i - \bar{P}\right)}{\sqrt{\sum_{i=1}^{N}\left(O_i - \bar{O}\right)^2\sum_{i=1}^{N}\left(P_i - \bar{P}\right)^2}}\right)^2$$

Simulation concept for model validation

A detailed description of stand and soil as well meteorological data are required for model validation at specific sites. The results of simulation runs of 4C using the stand and site description for model initialization and the meteorological data as driving forces were then tested against observed data in annual or daily time resolution.

From the datasets described in section '*stand data*' of this Appendix and section 3.2.2 of the main paper, nine sites in Europe with diverse species and site conditions have been selected which fulfill the requirements of providing enough input data while at the same time data for model validation is available (Table 9-4). The sets of observed data at the selected sites are different regarding variables and observation period. Table 9-5 gives an overview of the availability and number of observed data.

Table 9-4 Selected sites for the validation of 4C.

Site	Country	plot_id	Long. [°]	Lat. [°]	Altitude [m]	Biome	Species
Brasschaat	Belgium	BL15	4.52	51.30	16	temperate	pine
Collelongo	Italy	IT1	13.59	41.84	1560	mediterranean	beech
Hesse	France		7.06	48.67	300	temperate	beech
Hyytiälä	Finland		24.30	61.85	185	boreal	pine/spruce
Natteheide	Germany	DL1201	12.43	53.10	50	temperate	pine
Neusorgfeld	Germany	DL1205	13.57	51.78	75	temperate	pine
Solling B	Germany	DL304	9.57	51.75	504	temperate	beech
Solling F	Germany	DL305	9.57	51.75	508	temperate	spruce
Freising	Germany	DL919	11.66	48.41	508	temperate	beech

Validations Results: Statistical analysis of all sites

Here we present the results of the model validation using standard statistical measures as described in the section '*validation criteria*'. We validate three different types of output variables, namely the soil temperature, the soil water content, and fluxes (water and carbon). The exact values for each statistical measure can be found in Table 9-6 and Table 9-7. The results for individual sites can be quite different for each of the three components but generally the normalized errors are low and the Nash-Sutcliffe model efficiency and the correlation coefficients are high (see Fig. 9-2; Fig. 9-3; Fig. 9-4). For Hyytiälä, the NMRSE for the soil temperature are quite high (Fig. 9-2) and this will be discussed in the next section. The NRMSE and NMAE for Collelongo are also quite high (Fig. 9-2). Since this is a high mountain site, this maybe related to the uncertainties in the interpolation of the mean temperature and/or to the way snowfall and its heat isolation are modeled similarly as in Hyytiälä. High errors and low Nash-Sutcliffe model efficiency are noticeable for the NEE in Brasschaat (Fig. 9-4). There is however evidence that in Brasschaat, management interventions in the understorey have altered the carbon flux (Carrara et al. 2003) - a phenomenon not covered by 4C.

Table 9-5 Number of observed data used for the validation of 4C at the selected sites.

Site		Brasschaat	Collelongo	Hesse	Hyytiälä	Natteheide	Neusorgefeld	Solling B	Solling F	Freising
Time period		1997-1999	1997-2000	1996-2000	1997-2009	1994-2004	1994-2006	2000-2004	1995-2004	1999-2003
NEE		1095	1278	1580	4748	-	-	-	-	-
GPP		-	-	-	4748	-	-	-	-	-
TER		-	-	-	4748	-	-	-	-	-
AET		1095	1401	1687	4748	-	-	-	-	-
Water content vol% (depth in cm)	+2[1)]	-	-	-	4748	-	-	362	1563	-
	5	-	-	-	4748	-	-	-	-	684
	20[2)]	503	-	107	4748	2821	3226	-	1592	993
	50[3)]	503	-	107	4748	-	-	-	-	-
	70[4)]	503	-	-	-	2821	3226	357	554	993
	95[5)]	503	-	107	-	-	-	-	-	993
	140	-	-	-	-	-	-	-	-	991
Soil temperature °C (depth in cm)	+2[1)]	-	-	-	4748	-	-	882	-	-
	5[6)]	1757	-	1580	4748	-	-	938	1232	588
	10[7)]	1766	-	-	4748	3254	3226	882	1225	587
	30[8)]	-	1196	-	4748	-	-	980	1230	515
	70	-	-	-	-	3254	3226	-	-	503
	90	-	-	-	-	-	-	992	1230	515
	140[9)]	-	-	-	-	-	-	944	1229	515

NEE – Net Ecosystem Exchange, GPP – Gross Primary Production, TER – Total Ecosystem Respiration, AET – Actual Evapotranspiration

[1)]Organic layer, [2)]Brasschaat – 25 cm, Hesse – 15 cm, Hyytiälä – 18 cm, Freising – 30 cm, [3)]Hesse – 55 cm [4)]Brasschaat – 75 cm, [5)]Brasschaat – 100 cm, Freising – 90 cm, [6)]Brasschaat – 2 cm, Solling B, Solling F – 1 cm, [7)]Brasschaat – 9cm, , Hyytiälä – 18 cm, Neusorgefeld, Natteheide – 20 cm, [8)]Hyytiälä – 50 cm, Solling B, Solling F – 31 cm, [9)]Solling B, Solling F – 171 cm

Table 9-6 Values of the statistical analysis of the validation of 4C.

Site		Criteria	Brasschaat	Collelongo	Hesse	Hyytiälä	Natteheide	Neusorgfeld	Solling B	Solling F	Freising
NEE		NMAE	5.276	-0.644	-1.493	-1.297	-	-	-	-	-
		NRMSE	6.238	-0.918	-1.961	-1.861	-	-	-	-	-
		MEFF	0.047	0.776	0.613	0.601	-	-	-	-	
		CC	0.728	0.839	0.790	0.764	-	-	-	-	-
GPP		NMAE	-	-	-	0.319	-	-	-	-	-
		NRMSE	-	-	-	0.510	-	-	-	-	-
		MEFF	-	-	-	0.882	-	-	-	-	-
		CC	-	-	-	0.897	-	-	-	-	-
TER		NMAE	-	-	-	0.407	-	-	-	-	-
		NRMSE	-	-	-	0.516	-	-	-	-	-
		MEFF	-	-	-	0.839	-	-	-	-	-
		CC	-	-	-	0.857	-	-	-	-	-
AET		NMAE	0.549	0.710	0.308	0.379	-	-	-	-	-
		NRMSE	0.748	0.945	0.503	0.530	-	-	-	-	-
		MEFF	0.720	0.631	0.893	0.865	-	-	-	-	-
		CC	0.750	0.728	0.908	0.880	-	-	-	-	-
	+2[1)]	NMAE	-	-	-	0.229	-	-	0.141	0.190	-
		NRMSE	-	-	-	0.281	-	-	0.205	0.237	-
		MEFF	-	-	-	0.927	-	-	0.960	0.947	-
		CC	-	-	-	0.329	-	-	0.481	0.490	-
	5	NMAE	-	-	-	0.212	-	-	-	-	0.186
		NRMSE	-	-	-	0.281	-	-	-	-	0.256
		MEFF	-	-	-	0.926	-	-	-	-	0.938
		CC	-	-	-	0.407	-	-	-	-	0.672
	20[2)]	NMAE	0.261	-	0.343	0.195	0.199	0.230	-	0.159	0.090
		NRMSE	0.396	-	0.378	0.244	0.278	0.286	-	0.198	0.112
		MEFF	0.861	-	0.863	0.945	0.932	0.923	-	0.962	0.988
		CC	0.570	-	0.727	0.515	0.767	0.784	-	0.592	0.785
Water content vol% (depth in cm)	50[3)]	NMAE	0.288	-	0.260	0.195	-	-	-	-	-
		NRMSE	0.410	-	0.287	0.245	-	-	-	-	-
		MEFF	0.859	-	0.920	0.943	-	-	-	-	-
		CC	0.508	-	0.636	0.443	-	-	-	-	-
	70[4)]	NMAE	0.114	-	-	-	0.160	0.467	0.138	0.067	0.100
		NRMSE	0.128	-	-	-	0.221	0.513	0.156	0.105	0.131
		MEFF	0.984	-	-	-	0.954	0.747	0.976	0.989	0.983
		CC	0.539	-	-	-	0.646	0.544	0.665	0.377	0.788
	95[5)]	NMAE	0.132	-	0.350	-	-	-	-	-	0.121
		NRMSE	0.153	-	0.356	-	-	-	-	-	0.154
		MEFF	0.977	-	0.874	-	-	-	-	-	0.977
		CC	0.522	-	0.472	-	-	-	-	-	0.788
	140	NMAE	-	-	-	-	-	-	-	-	0.102
		NRMSE	-	-	-	-	-	-	-	-	0.127
		MEFF	-	-	-	-	-	-	-	-	0.984
		CC	-	-	-	-	-	-	-	-	0.698

Site		Criteria	Brasschaat	Collelongo	Hesse	Hyytiälä	Natteheide	Neusorgfeld	Solling B	Solling F	Freising
Soil temperature °C (depth in cm)	+2[1)]	NMAE	-	-	-	0.308	-	-	0.199	-	-
		NRMSE	-	-	-	0.844	-	-	0.257	-	-
		MEFF	-	-	-	0.733	-	-	0.951	-	-
		CC	-	-	-	0.782	-	-	0.956	-	-
	5[6)]	NMAE	0.150	-	0.155	0.301	-	-	0.161	0.243	0.237
		NRMSE	0.188	-	0.193	0.969	-	-	0.211	0.328	0.289
		MEFF	0.971	-	0.969	0.651	-	-	0.967	0.926	0.931
		CC	0.950	-	0.964	0.698	-	-	0.963	0.883	0.934
	10[7)]	NMAE	0.166	-	-	0.176	0.168	0.168	0.170	0.214	0.204
		NRMSE	0.208	-	-	0.778	0.207	0.213	0.212	0.293	0.248
		MEFF	0.962	-	-	0.735	0.965	0.966	0.965	0.936	0.947
		CC	0.939	-	-	0.734	0.972	0.970	0.958	0.882	0.946
	30[8)]	NMAE	-	0.719	-	0.152	-	-	0.136	0.200	0.161
		NRMSE	-	0.798	-	0.801	-	-	0.178	0.267	0.190
		MEFF	-	0.734	-	0.687	-	-	0.974	0.946	0.970
		CC	-	0.951	-	0.629	-	-	0.947	0.891	0.967
	70	NMAE	-	-	-	-	0.171	0.303	-	-	0.069
		NRMSE	-	-	-	-	0.184	0.333	-	-	0.081
		MEFF	-	-	-	-	0.970	0.906	-	-	0.994
		CC	-	-	-	-	0.982	0.946	-	-	0.987
	90	NMAE	-	-	-	-	-	-	0.126	0.169	0.054
		NRMSE	-	-	-	-	-	-	0.152	0.222	0.064
		MEFF	-	-	-	-	-	-	0.980	0.958	0.996
		CC	-	-	-	-	-	-	0.951	0.881	0.992
	140[9)]	NMAE	-	-	-	-	-	-	0.063	0.140	0.055
		NRMSE	-	-	-	-	-	-	0.079	0.172	0.055
		MEFF	-	-	-	-	-	-	0.994	0.974	0.996
		CC	-	-	-	-	-	-	0.975	0.919	0.977

Footnotes see Table 9-5

Table 9-7 Linear regression coefficients of modeled versus observed data.

Site		Coefficient	Brasschaat	Collelongo	Hesse	Hyytiälä	Natteheide	Neusorgefeld	Solling B	Solling F	Freising
NEE		a	-1.167	-4.805	-0.9825	-0.441	-	-	-	-	-
		b	0.407	0.658	0.462	0.438	-	-	-	-	-
		R^2	0.530	0.704	0.597	0.414	-	-	-	-	
GPP		a	-	-	-	0.186	-	-	-	-	-
		b	-	-	-	0.531	-	-	-	-	-
		R^2	-	-	-	0.577	-	-	-	-	-
TER		a	-	-	-	-0.044	-	-	-	-	-
		b	-	-	-	0.531	-	-	-	-	-
		R^2	-	-	-	0.606	-	-	-	-	-
AET		a	0.431	0.654	0.300	-0.030	-	-	-	-	-
		b	0.740	0.809	0.577	1.075	-	-	-	-	-
		R^2	0.562	0.593	0.481	0.459	-	-	-	-	-
Water content vol% (depth in cm)	+2[1]	a	-	-	-	21.969	-	-	22.295	19.123	-
		b	-	-	-	0.215	-	-	0.281	0.367	-
		R^2	-	-	-	0.109	-	-	0.232	0.240	-
	5	a	-	-	-	21.239	-	-	-	-	7.962
		b	-	-	-	0.273	-	-	-	-	0,846
		R^2	-	-	-	0.231	-	-	-	-	0.448
	20[2]	a	8.749	-	-	26.931	13.19	-3.842	-	14.459	-0.900
		b	0.204	-	-	0.237	0.376	1.153	-	0.319	1.028
		R^2	0.325	-	-	0.265	0.324	0.615	-	0.107	0.616
	50[3]	a	14.947	-	-	38.895	-	-	-	-	-
		b	0.117	-	-	0.067	-	-	-	-	-
		R^2	0.258	-	-	0.196	-	-	-	-	-
	70[4]	a	22.757	-	-	-	4.706	-1.162	24.66	29.531	5.1054
		b	0.130	-	-	-	0.520	0.676	0.368	0.189	0.904
		R^2	0.291	-	-	-	0.417	0.296	0.442	0.060	0.620
	95[5]	a	23.422	-	-	-	-	-	-	-	4.379
		b	0.107	-	-	-	-	-	-	-	0.948
		R^2	0.273	-	-	-	-	-	-	-	0.621
	140	a	-	-	-	-	-	-	-	-	18.994
		b	-	-	-	-	-	-	-	-	0.427
		R^2	-	-	-	-	-	-	-	-	0.487
Soil temperature °C (depth in cm)	+2[1]	a	-	-	-	0.147	-	-	-2.312	-	-
		b	-	-	-	1.013	-	-	1.269	-	-
		R^2	-	-	-	0.941	-	-	0.890	-	-
	5[6]	a	-1.874	-	-	0.052	-	-	-1.486	0.513	-2.942
		b	1.092	-	-	1.046	-	-	1.095	0.876	1.327
		R^2	0.902	-	-	0.951	-	-	0.927	0.872	0.904
	10[7]	a	-2.427	-	-	0.298	-1.931	-1.707	-0.486	0.202	-4.021
		b	1.087	-	-	0.969	1.066	1.060	1.003	0.912	1.272
		R^2	0.882	-	-	0.973	0.957	0.958	0.962	0.865	0.929
	30[8]	a	-	3.843	-	-0.119	-	-	0.603	0.355	-0.819
		b	-	0.867	-	1.020	-	-	0.877	0.908	1.149
		R^2	-	0.910	-	0.961	-	-	0.961	0.927	0.964
	70	a	-	-	-	-	-0.283	-0.179	-	-	-0.5412

Site		Coefficient	Brasschaat	Collelongo	Hesse	Hyytiälä	Natteheide	Neusorgefeld	Solling B	Solling F	Freising
		b	-	-	-	-	0.858	0.710	-	-	1.060
		R^2	-	-	-	-	0.967	0.890	-	-	0.982
	90	a	-	-	-	-	-	-	2.197	0.414	-0.052
		b	-	-	-	-	-	-	0.676	0.979	1.011
		R^2	-	-	-	-	-	-	0.856	0.951	0.960
	140[9)]	a	-	-	-	-	-	-	0.182	0.682	0.854
		b	-	-	-	-	-	-	0.932	1.028	0.912
		R^2	-	-	-	-	-	-	0.927	0.946	0.892

Footnotes see Table 9-5

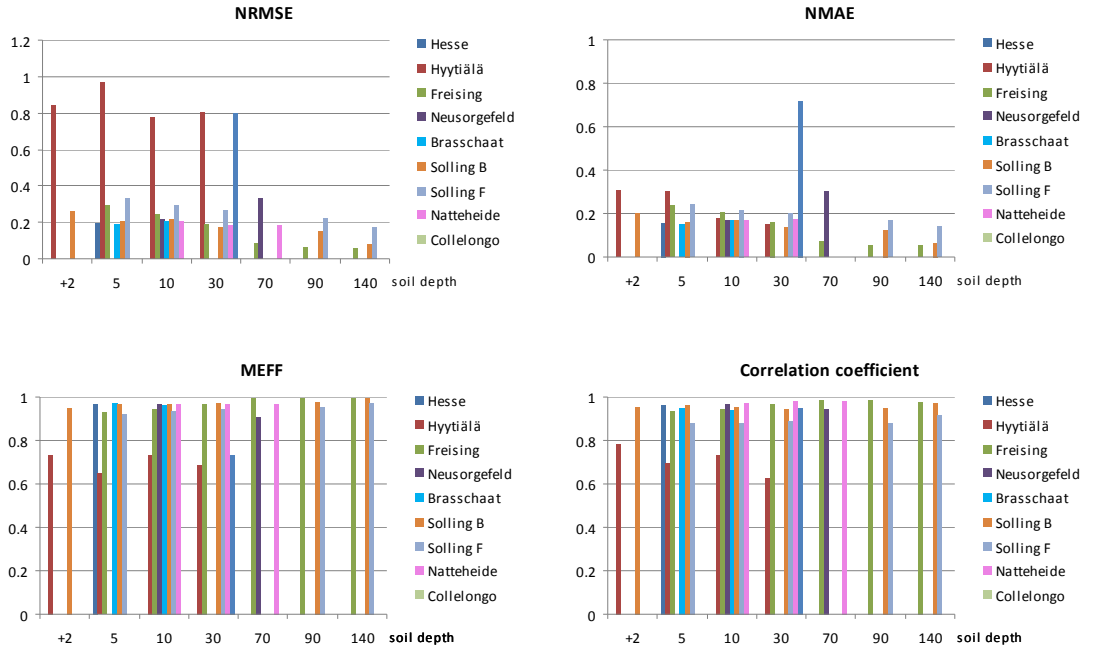

Fig. 9-2 Normalized root mean square error (NRMSE), normalized mean absolute error (NMAE), Nash–Sutcliffe model efficiency coefficient (MEFF), correlation coefficient of soil temperature at several depths for the nine validation sites of 4C.

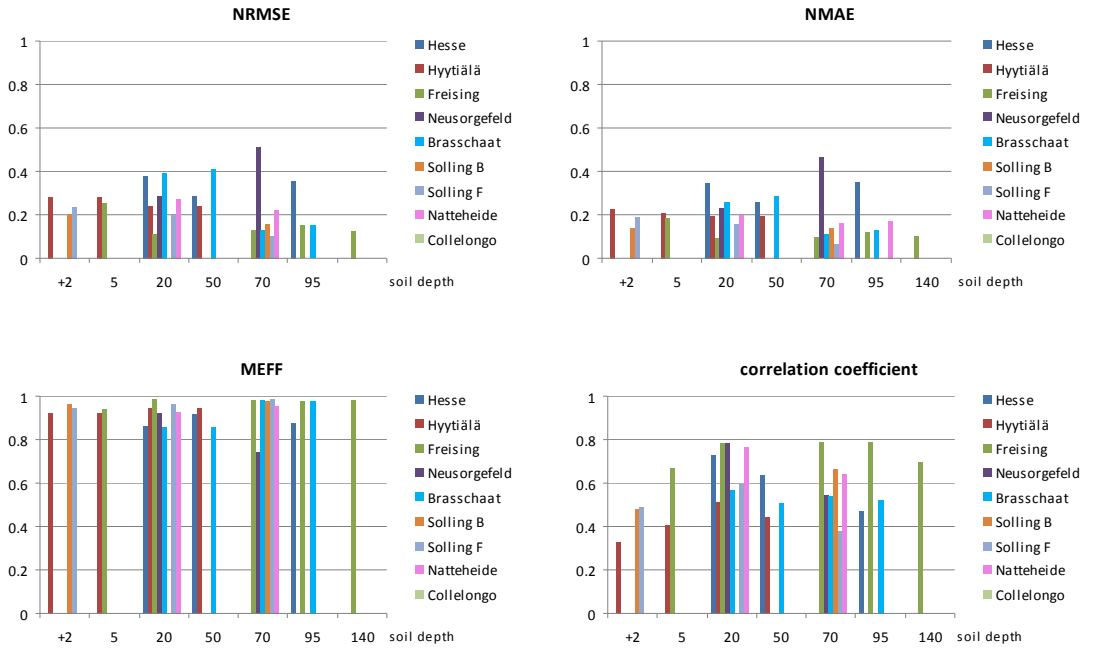

Fig. 9-3 Normalized root mean square error (NRMSE), normalized mean absolute error (NMAE), Nash–Sutcliffe model efficiency coefficient (MEFF), correlation coefficient of soil water content at several depths for the nine validation sites of 4C.

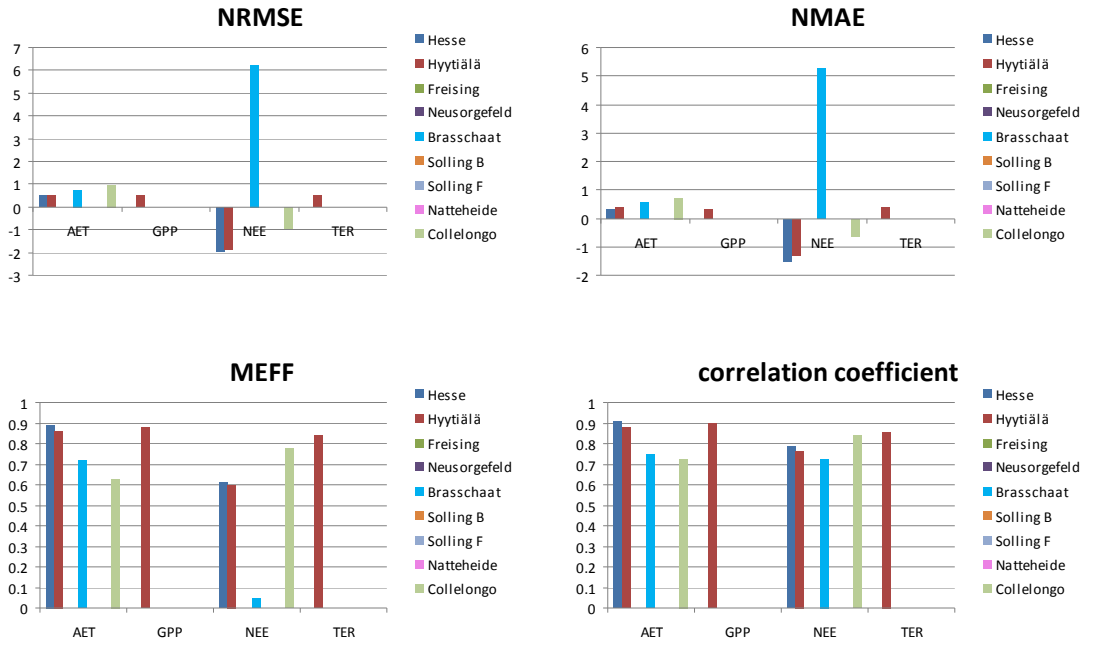

Fig. 9-4 Normalized root mean square error (NRMSE), normalized mean absolute error (NMAE), Nash–Sutcliffe model efficiency coefficient (MEFF), correlation coefficient of actual evapotranspiration (AET), gross primary productivity (GPP), net ecosystem exchange (NEE), and total ecosystem respiration (TER) for the nine validation sites of 4C.

Validations Results: Model validation at the Hyytiälä site

We complement the statistical analysis with a graphical analysis of the annual course of soil temperature, soil water and the carbon and water fluxes for the Hyytiälä site for which the largest and longest data set is available. Note that all measured data has been gap-filled by standard methods.

Fig. 9-5 and Fig. 9-6 show that the simulated soil temperature follows the annual course of the measured values and that no systematic bias exists. Only the temperature peaks in summer and winter are sometimes overestimated. In the winter this maybe related to a premature simulation of the first snow. In soil depths of 50cm, the heat conductance seems to be too high in some winters (2001, 2002, and 2003). In general, there is a good correspondence between simulated and observed values.

The soil water content in the organic layer is mostly not correctly simulated by 4C (Fig. 9-7; Fig. 9-8). This has several reasons. The parameter uncertainty in the organic layer is larger than for the mineral soil. The soil model works on a daily time step and the model treats all soil layers according to the same physical principles but physical processes important for the organic layer such as hysteresis-effects are not covered. In the lower soil layers (5 and 18cm), 4C meets the annual pattern of the measured values but the errors apparent in the organic layer propagate into these layers. However, the water reductions in the summer are quite realistically simulated and no systematic bias occurs (Fig. 9-7; Fig. 9-8). In 50cm soil depth, 4C overestimates the soil water content (Fig. 9-7) since the transpiration demand of the trees is already covered with water from the upper soil layers. This hints towards a slight underestimation of the transpiration demand.

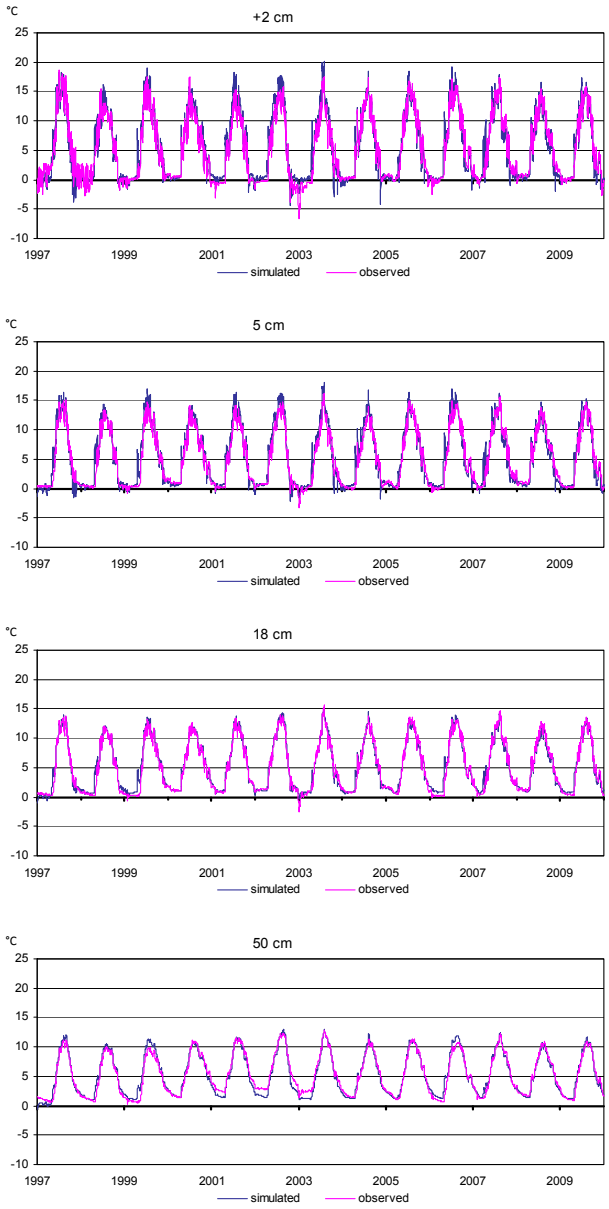

Fig. 9-5 Simulated and observed soil temperature (1997-2009) in four soil depths in Hyytiälä.

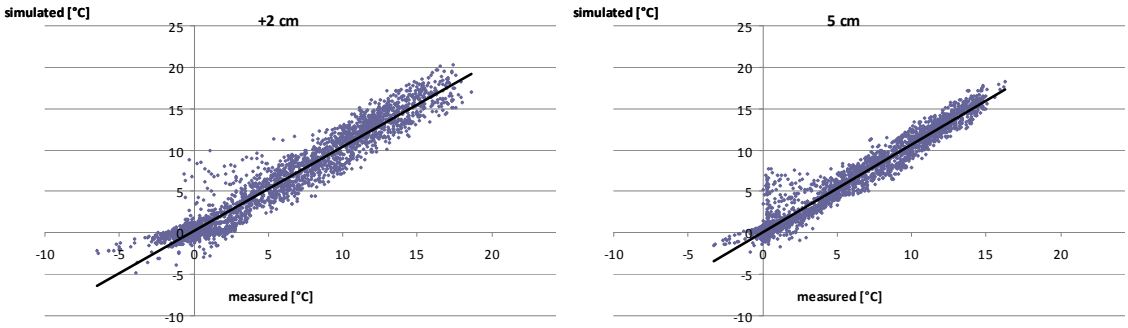

Fig. 9-6 Simulated versus observed soil temperature in Hyytiälä at two soil depths and regression lines (for the parameter values see Table 9-7).

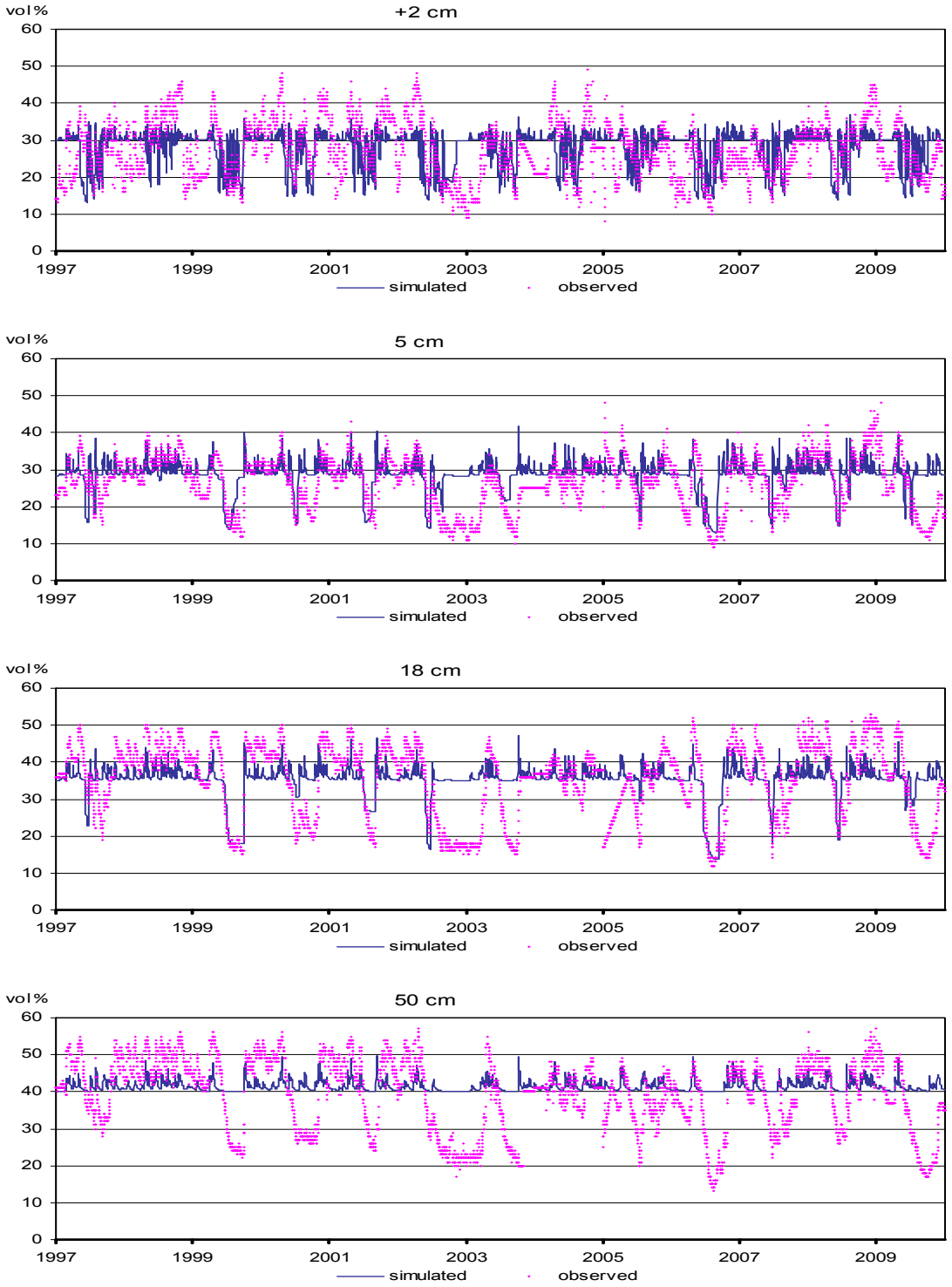

Fig. 9-7 Simulated and observed soil water content (1997-2009) in four soil depths in Hyytiälä.

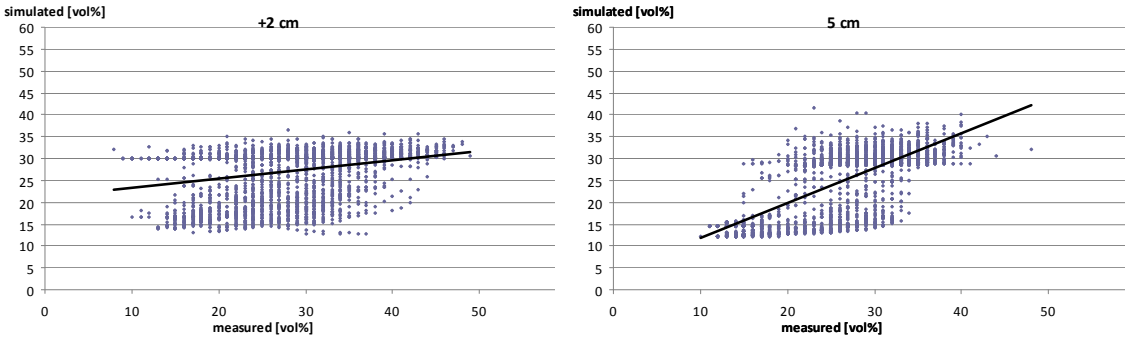

Fig. 9-8 Simulated versus observed soil water content in Hyytiälä at two soil depths and regression lines (for the parameter values see Table 9-7).

The carbon and water fluxes are mostly underestimated by 4C. This is apparent in the annual values of GPP and AET (Fig. 9-9). The analysis of the daily values shows that this is especially the case for small values (Fig. 9-10) and the residual plots show that a systematic underestimation of NEE at low temperatures causes this deviation between measured and observed fluxes (Fig. 9-11; Fig. 9-12). The residual plots also show that the variation of the residuals increases with increasing temperature which hints at a temperature-dependency of the residuals (Fig. 9-12).

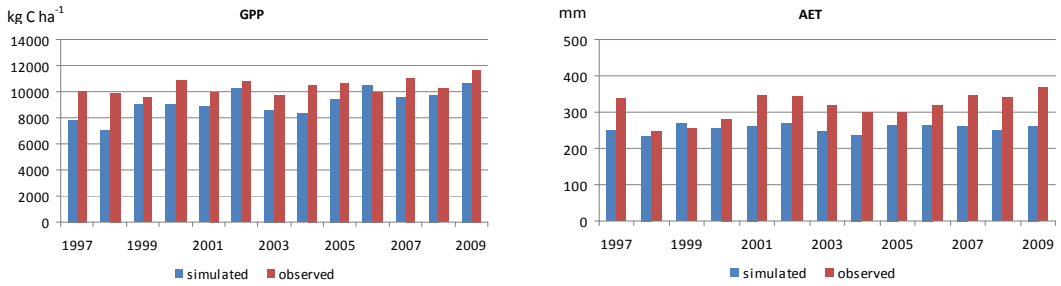

Fig. 9-9 Annual observed and simulated GPP (left) and AET (right) for the time period 1997-2009 in Hyytiälä.

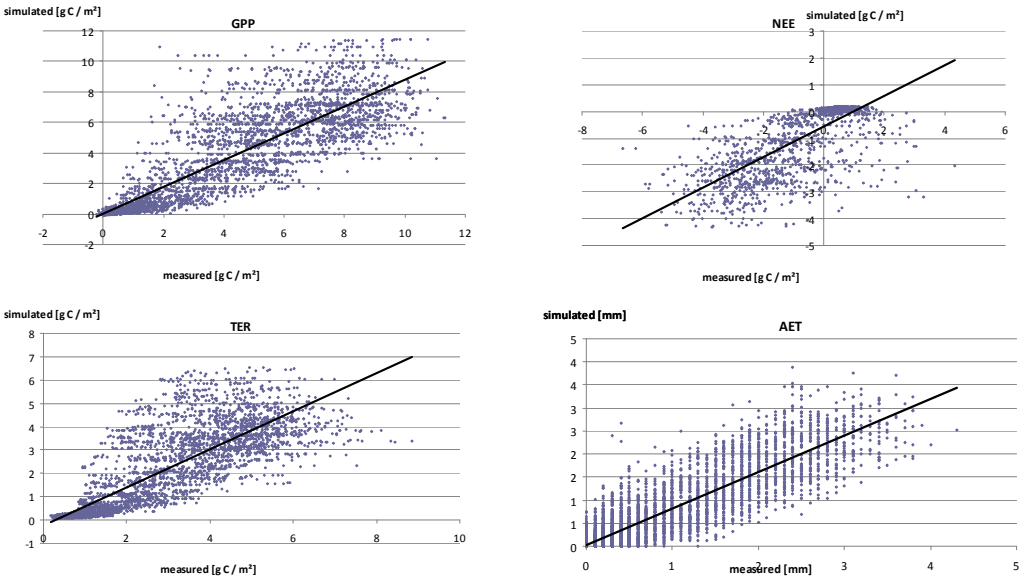

Fig. 9-10 Simulated versus observed daily GPP, NEE, TER, and AET in Hyytiälä and regression lines (for the parameter values see Table 9-7).

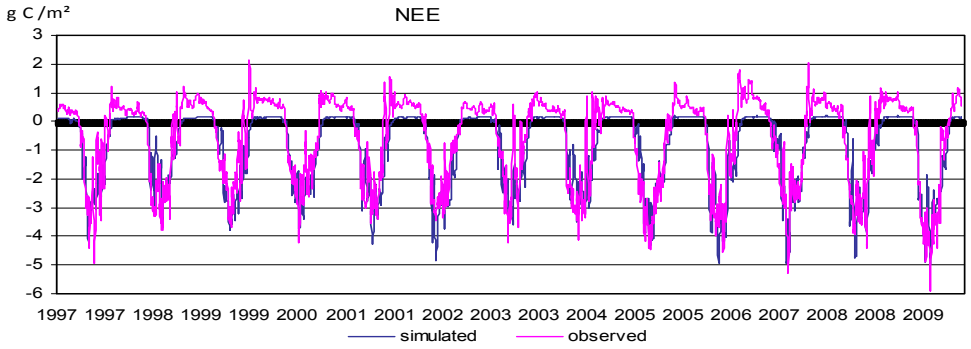

Fig. 9-11 Seven-day moving average of daily simulated and observed NEE in Hyytiälä.

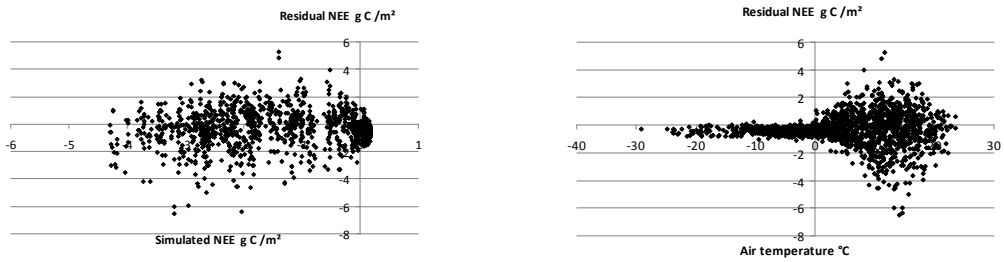

Fig. 9-12 Residuals of the NEE versus simulated NEE (left) and versus air temperature (right).

Validation: Concluding remarks

The validation statistics as well as the graphical comparison of measured and simulated values of different parameters show satisfactory results, which provide evidence that the model application at a great variety of sites for the considered species in Europe will give plausible results.

Climate change simulation results

Fig. 9-13 to Fig. 9-18 show the changes in NPP for each site and for each RCM/GCM combination, CO_2-emission scenario, realization and time slice individually.

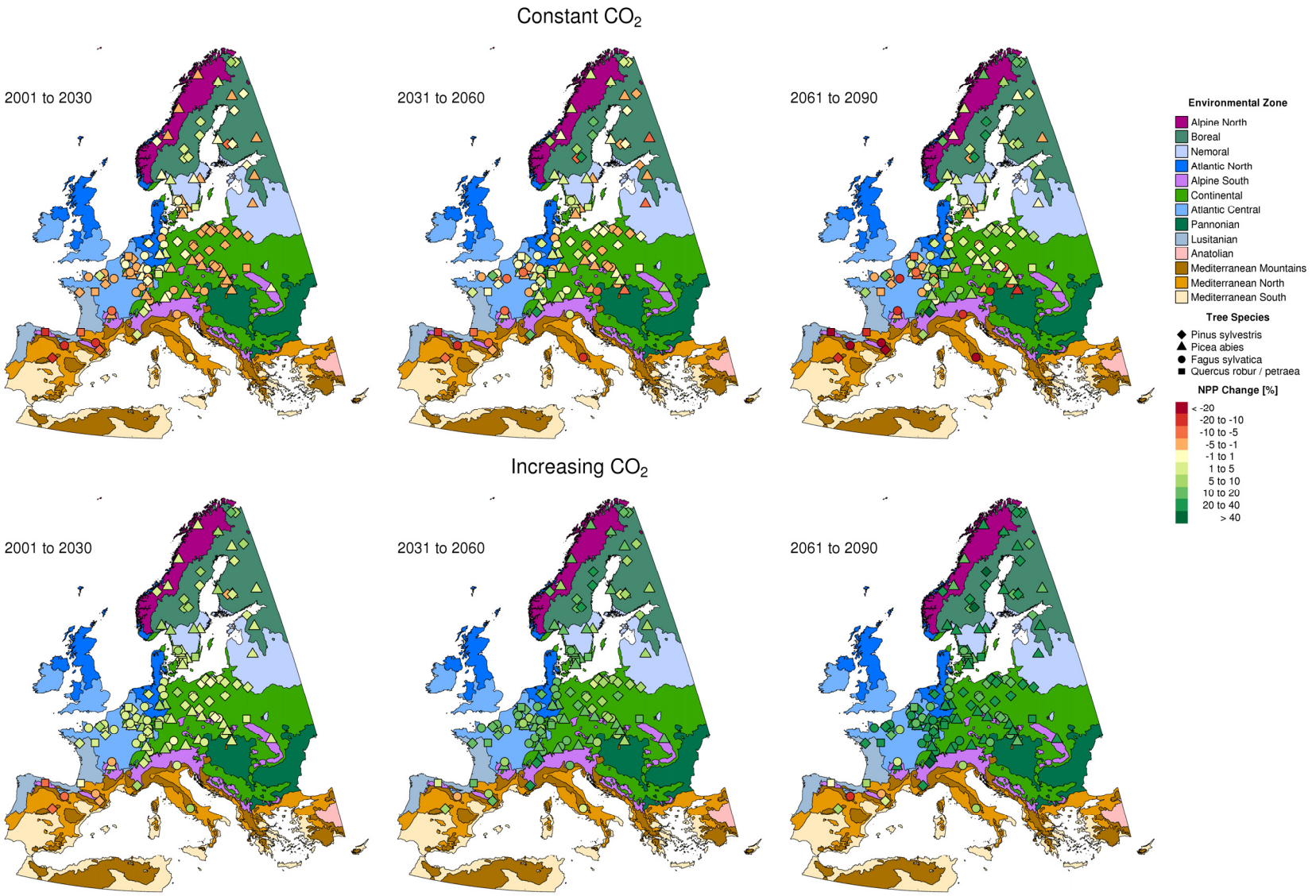

Fig. 9-13 Change in net primary productivity (NPP) for each site for the CCLM/ECHAM5 A1B realization 1 climate change scenario for the time slices 2001-2030, 2031-2060 and 2061-2090 with constant and increasing CO_2. The environmental zones follow the classification of Metzger et al. (2005).

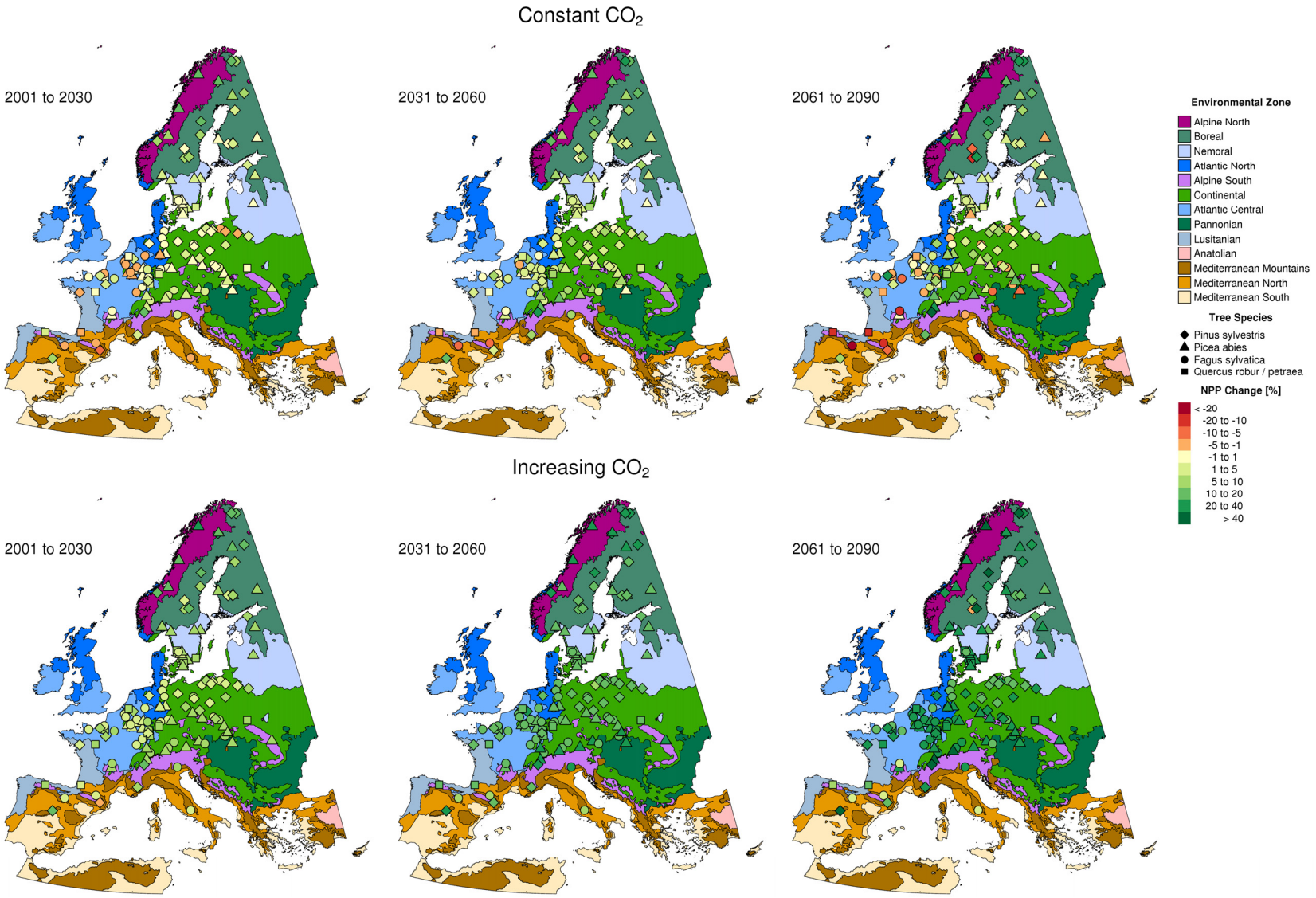

Fig. 9-14 Change in net primary productivity (NPP) for each site for the CCLM/ECHAM5 A1B realization 2 climate change scenario for the time slices 2001-2030, 2031-2060 and 2061-2090 with constant and increasing CO_2. The environmental zones follow the classification of Metzger et al. (2005).

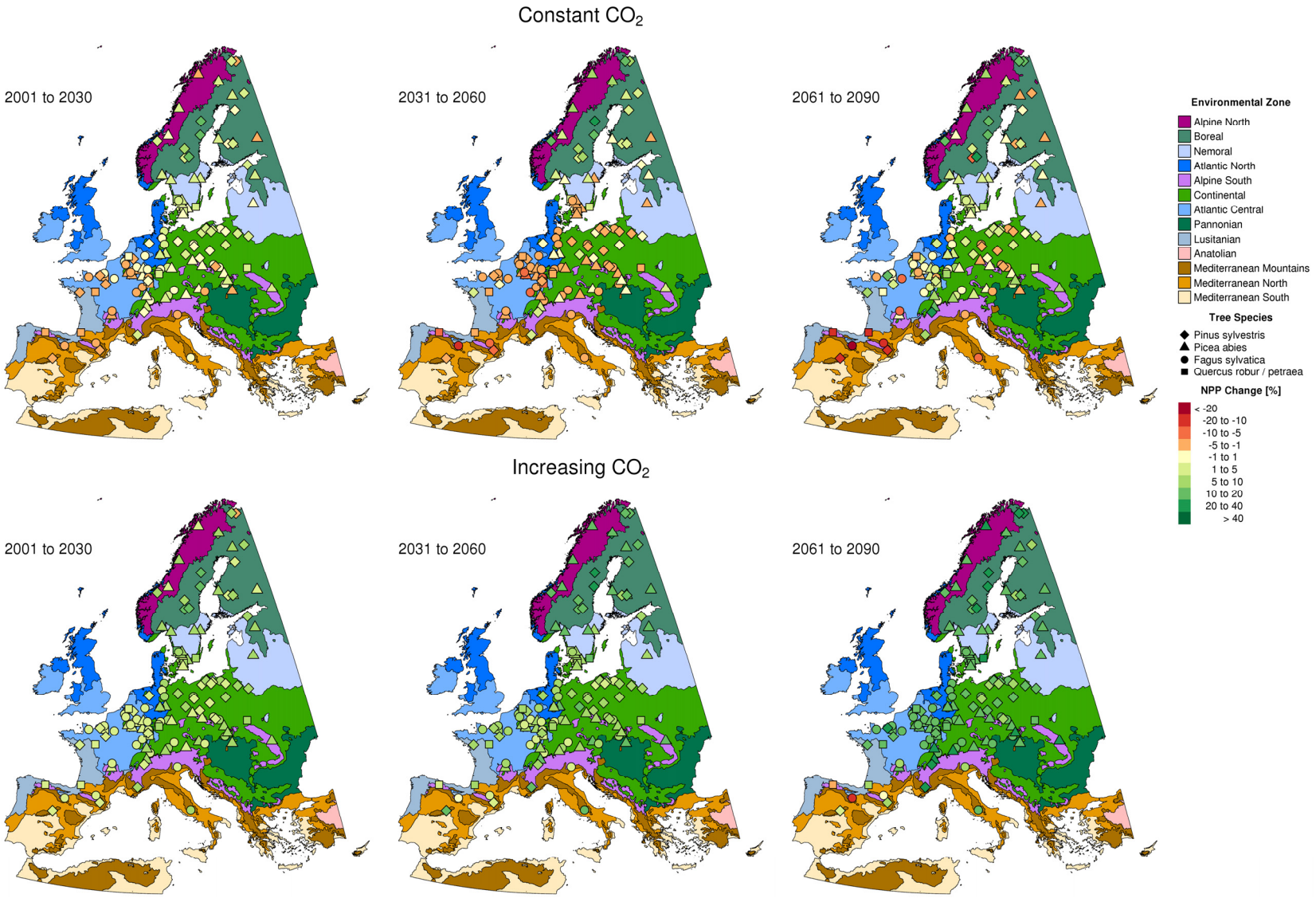

Fig. 9-15 Change in net primary productivity (NPP) for each site for the CCLM/ECHAM5 B1 realization 1 climate change scenario for the time slices 2001-2030, 2031-2060 and 2061-2090 with constant and increasing CO_2. The environmental zones follow the classification of Metzger et al. (2005).

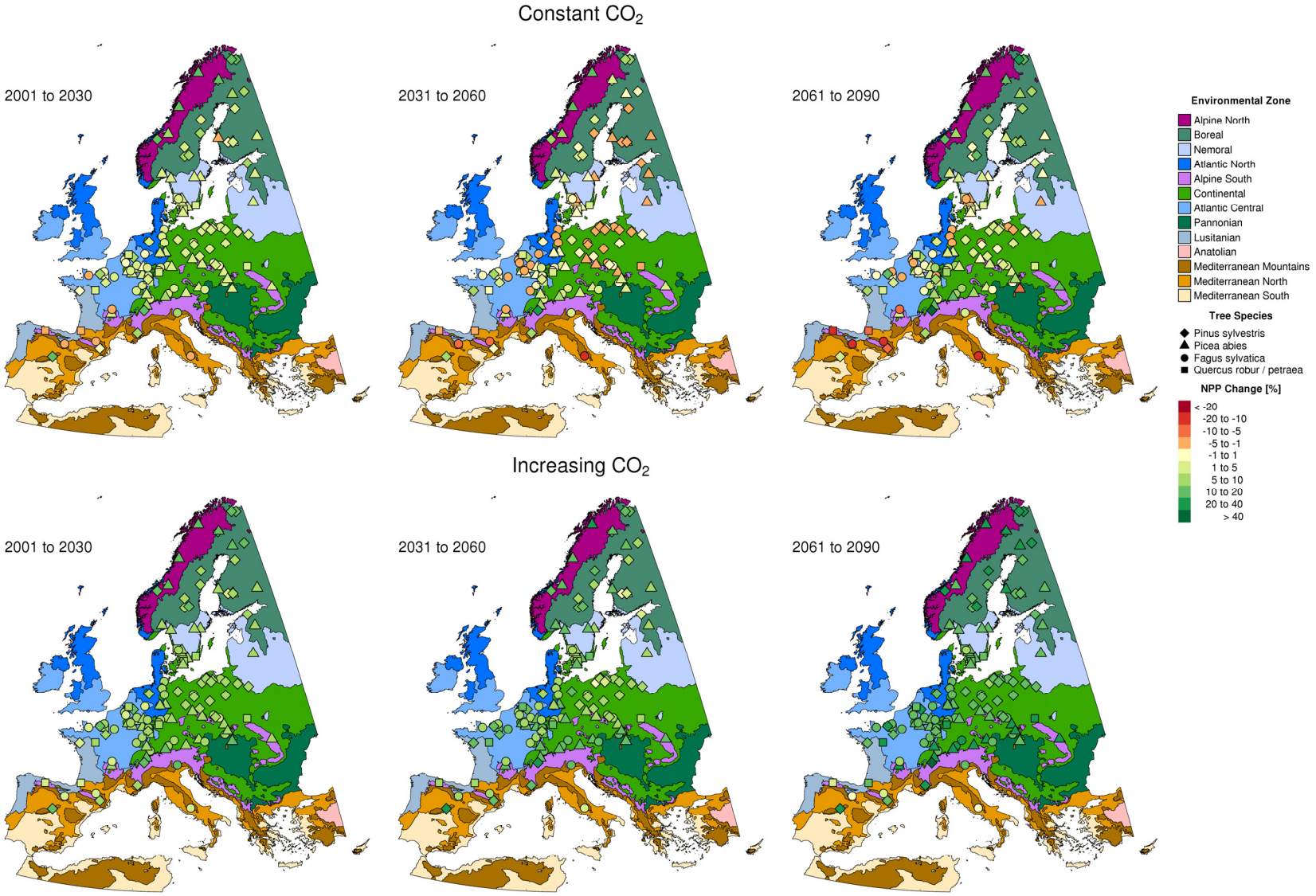

Fig. 9-16 Change in net primary productivity (NPP) for each site for the CCLM/ECHAM5 B1 realization 2 climate change scenario for the time slices 2001-2030, 2031-2060 and 2061-2090 with constant and increasing CO_2. The environmental zones follow the classification of Metzger et al. (2005).

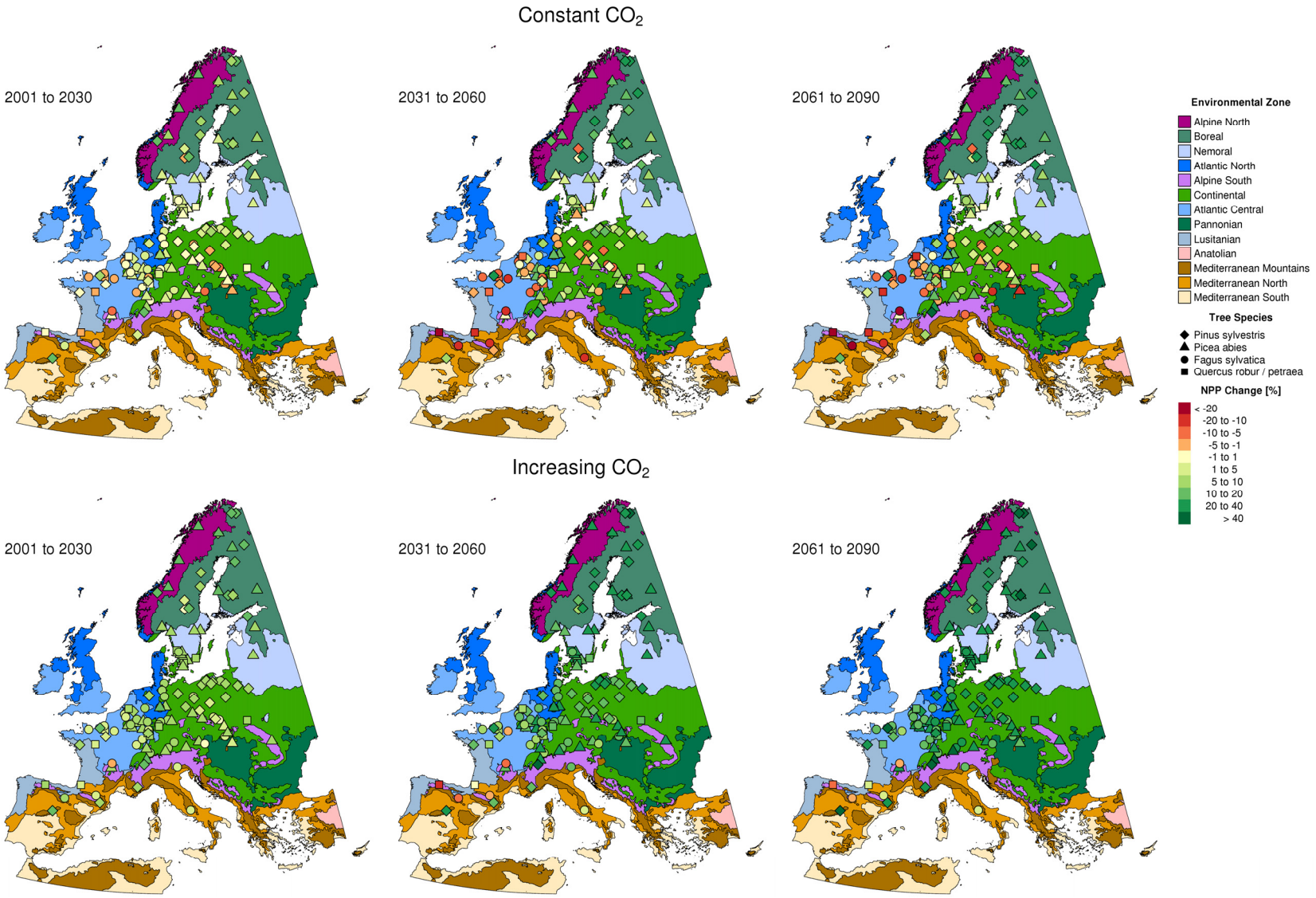

Fig. 9-17 Change in net primary productivity (NPP) for each site for the HadRM3/HadCM3 A1B realization 1 climate change scenario for the time slices 2001-2030, 2031-2060 and 2061-2090 with constant and increasing CO_2. The environmental zones follow the classification of Metzger et al. (2005).

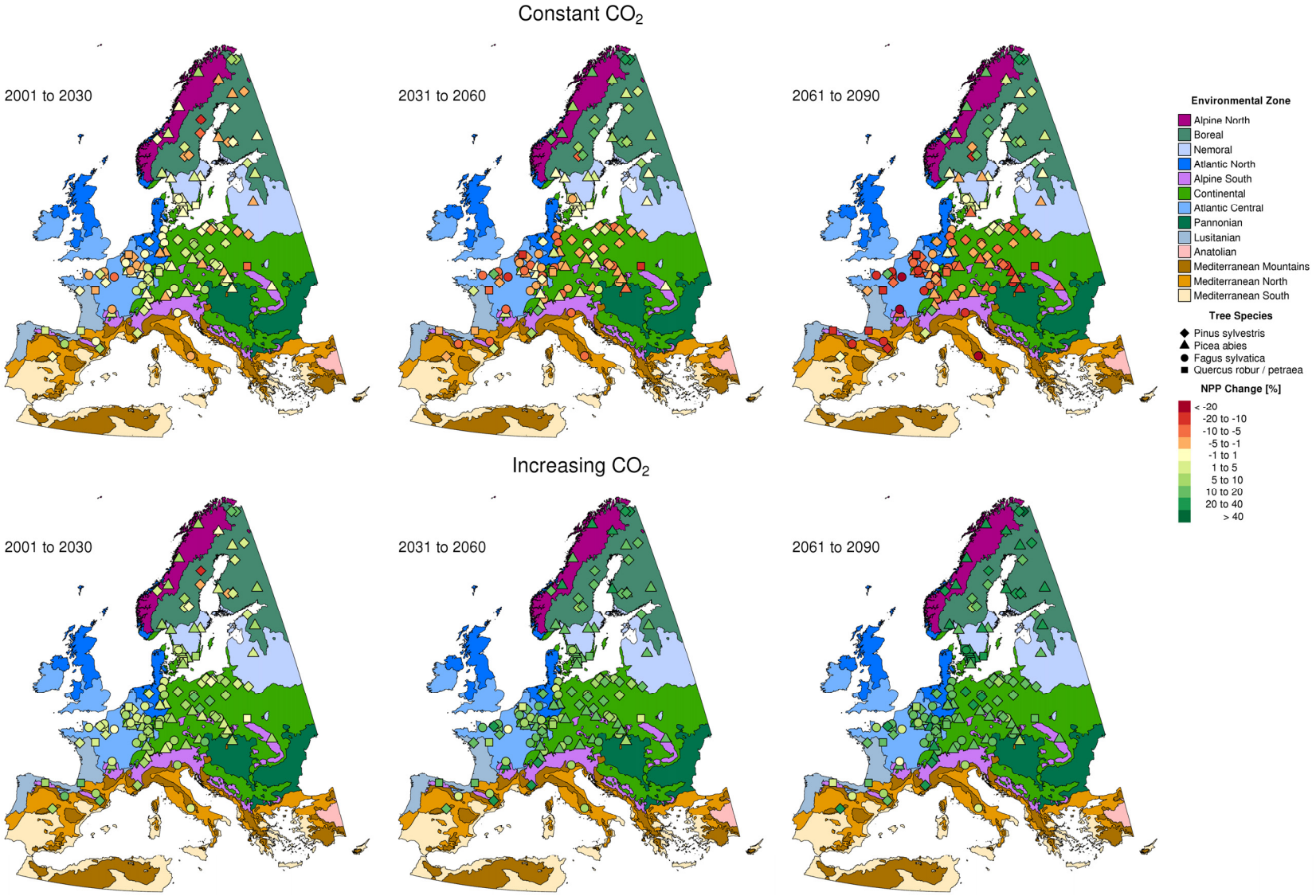

Fig. 9-18 Change in net primary productivity (NPP) for each site for the HIRHAM3/Arpège A1B realization 1 climate change scenario for the time slices 2001-2030, 2031-2060 and 2061-2090 with constant and increasing CO_2. The environmental zones follow the classification of Metzger et al. (2005).

9.3 Appendix to chapter 4

Table 9-8 shows the standard parameter values of 4C that have been varied in this study.

Table 9-8 The standard parameter values of 4C that have been varied in this study.

4C Name	Unit	Main process	Standard value	Description	Source
pfext	-	Allocation	0.6	Extinction coefficient	Expert Assessment
sigman	[yr^{-1}]	Allocation	0.03	Root activity rate (N uptake)	Modified from data communicated by M. Sonntag, S. Luoma, R. Sievänen
psf	[day^{-1}]	Allocation	0.31	Senescence rates: foliage	Modified from Sonntag 1998; Bossel 1994; Mäkelä 1997
pss	[day^{-1}]	Allocation	0.04	Senescence rates: sapwood	Modified from data communicated by M. Sonntag, S. Luoma, R. Sievänen
psr	[day^{-1}]	Allocation	0.5	Senescence rates: fine roots	Modified from Sonntag 1998; Bossel 1994; Mäkelä 1997 and from data communicated by M. Sonntag, S. Luoma, R. Sievänen
pcnr	[kg N kg C^{-1}]	Allocation	0.0079	N/C ratio of biomass	Modified from Sonntag 1998; Bossel 1994
ncon_fol	[mg g^{-1}]	Allocation	13.46	N concentration of foliage	Modified from Jacobsen et al. 2002
ncon_frt	[mg g^{-1}]	Allocation	7.44	N concentration of fine roots	Modified from Jacobsen et al. 2002
ncon_crt	[mg g^{-1}]	Allocation	1.77	N concentration of coarse roots	Modified from Jacobsen et al. 2002
ncon_tbc	[mg g^{-1}]	Allocation	3.61	N concentration of twigs and branches	Modified from Jacobsen et al. 2002
ncon_stem	[mg g^{-1}]	Allocation	1.09	N concentration of stemwood	Modified from Jacobsen et al. 2002
reallo_fol	-	Allocation	0.1	Reallocation parameter of foliage	Expert Assessment
reallo_frt	-	Allocation	0.1	Reallocation parameter of fine roots	Expert Assessment
alphac	-	Allocation	0.46	Ratio of coarse wood (twigs, branches, roots) to sapwood	Expert Assessment
cr_frac	-	Allocation	0.6	Fraction of twigs, branches and coarse roots that is coarse roots	Modified from Cannell 1982
pnus	[kg cm^{-2}]	Allocation	0.05	Foliage mass to sapwood area ratio (pipe model)	Modified from Berninger & Nikinmaa 1994; Mäkelä et al. 1995; Mencuccini & Grace 1995; Kaipianen & Hari 1995; Leemans & Prentice 1989 and from data communicated by M. Sonntag, S. Luoma, R. Sievänen
pha_v1	-	Allocation	206	Parameter for non-linear height-foliage relationship	Modified from data of Dengler 1937; Burger 1948; Lyr et al. 1964; Claesson et al. 2001
pha_v2	-	Allocation	0.03177	Parameter for non-linear height-foliage relationship	Modified from data of Dengler 1937; Burger 1948; Lyr et al. 1964; Claesson et al. 2001
pha_v3	-	Allocation	0.877	Parameter for non-linear height-foliage relationship	Modified from data of Dengler 1937; Burger 1948; Lyr et al. 1964; Claesson et al. 2001
crown_a	[m cm^{-1}]	Allocation	0.05213	Parameter to calculate crown radius from DBH	Modified from data of Burger 1948
crown_b	[m]	Allocation	0.48139	Parameter to calculate crown radius from DBH	Modified from data of Burger 1948
crown_c	[m]	Allocation	10	Parameter to calculate crown radius from DBH	Expert Assessment
ceppot_spe	[mm m^{-2} leaf area]	Canopy	0.9	Interception capacity parameter	Modified from Jansson et al. 1991 and from Level-II data
k_opm_fol	[day^{-1}]	Decomposition	0.025	Mineralization constant of foliage litter	Modified from Bergmann 1998

4C Name	Unit	Main process	Standard value	Description	Source
k_syn_fol	-	Decomposition	0.5	Synthesis coefficient of foliage litter	Modified from Bergmann 1998
k_opm_frt	[day^{-1}]	Decomposition	0.035	Mineralization constant of fine roots	Modified from Bergmann 1998
k_syn_frt	-	Decomposition	0.5	Synthesis coefficient of fine roots	Modified from Bergmann 1998
k_opm_crt	[day^{-1}]	Decomposition	0.0009	Mineralization constant of coarse roots	Modified from Bergmann 1998
k_opm_tb	[day^{-1}]	Decomposition	0.006	Mineralization constant of twigs and branches litter	Modified from Bergmann 1998
k_syn_tb	-	Decomposition	0.5	Synthesis coefficient of twigs and branches litter	Modified from Bergmann 1998
k_opm_stem	[day^{-1}]	Decomposition	0.0005	Mineralization constant of stemwood	Modified from Bergmann 1998
respcoeff	-	NPP calculation	0.52	Respiration coefficient, i.e. fraction of gross production respired by plant	Modified from Landsberg &Waring 1997
psla_min	[m2 kg^{-1} DW]	Photosynthesis	4	Minimum specific one-sided leaf area	Modified from Sonntag 1998; Bossel 1994; Bugmann 1994; Mäkelä 1995; Virtanen 1993 and from data communicated by M. Sonntag, S. Luoma, R. Sievänen
psla_a	[m2 kg^{-1} DW]	Photosynthesis	1	Light dependent specific one-sided leaf area	Modified from Lyr et al. 1964
phic	-	Photosynthesis	0.9	Efficiency parameter, different for evergreen/deciduous	Modified from Bugmann 1994
kco2_25	[Pa]	Photosynthesis	30	Michaelis constant for CO_2 (base 25 °C)	Haxeltine & Prentice 1996
ko2_25	[kPa]	Photosynthesis	60	Inhibition constant of O_2 (base 25 °C)	Modified from Haxeltine & Prentice 1996
pc_25	-	Photosynthesis	3400	CO_2/O_2 specificity ratio (base 25 °C)	Modified from Haxeltine & Prentice 1996
Q10_kco2	-	Photosynthesis	2.1	Q10 coefficients (acclimated to 25 °C)	Haxeltine & Prentice 1996
Q10_ko2	-	Photosynthesis	1.2	Q10 coefficients (acclimated to 25 °C)	Haxeltine & Prentice 1996
Q10_pc	-	Photosynthesis	0.57	Q10 coefficients (acclimated to 25 °C)	Haxeltine & Prentice 1996
pb	-	Photosynthesis	0.01	Rd to Vm ratio	Modified from Haxeltine & Prentice 1996
Nresp	[yr kg^{-1} ha^{-1}]	Photosynthesis	0.0062	Slope of photosynthesis response to Nitrogen(N-limitation)	Modified from Lindner 1998

9.4 Appendix to chapter 5

The results of the individual model runs associated with this chapter can be found in the online version of the published article at http://dx.doi.org/10.1016/j.foreco.2012.09.043.

Erklärung

Ich erkläre, dass ich die vorliegende Arbeit selbständig und nur unter Verwendung der angegebenen Literatur und Hilfsmittel angefertigt habe.

Berlin, den 21.12.2012

Christopher Reyer